Domestic chicks perceive stereokinetic illusions

Elena Clara, Lucia Regolin, Mario Zanforlin
Department of General Psychology, University of Padua, via Venezia 8, I 35131 Padua, Italy; e-mail: lucia.regolin@unipd.it
Giorgio Vallortigara
Department of Psychology and B.R.A.I.N. Centre for Neuroscience, University of Trieste, via S Anastasio 12, I 34123 Trieste, Italy
Received 27 January 2005, in revised form 16 August 2005; published online 9 June 2006

Abstract. Stereokinetic illusions occur when certain 2-D patterns are set in slow rotation in a plane perpendicular to the line of sight. Such phenomena have never been investigated in animal species other than our own. We used the domestic chick (Gallus gallus) to check whether these illusions are experienced by non-human species, taking advantage of filial imprinting. Newly hatched visually naive chicks were individually exposed for 4 h to 2-D stimuli producing, to a human observer, the perception of a stereokinetic cone (experiment 1) or of a stereokinetic cylinder (experiment 2). Thereafter, each chick underwent a free-choice test between a solid 3-D cone and a solid 3-D cylinder. A control group of newly hatched but not imprinted chicks underwent the same testing procedure, to check for the presence of any spontaneous preference for one or other of the two solid objects. Imprinted chicks approached the 3-D stimulus closely resembling the stimulus they had been exposed to during imprinting (the cone in experiment 1 and the cylinder in experiment 2). Non-imprinted chicks did not show any preference. These results suggest that domestic chicks experience stereokinetic illusions.

DOI:10.1068/p5420

1 Introduction
The human visual system shows a striking ability to extract 3-D shape information from 2-D transformations of the image (Wallach and O’Connell 1953; Ullman 1979). One peculiar example of this ‘structure-from-motion’ perception is the phenomenon dubbed ‘stereokinetic effect’ (Musatti 1924; Bressan and Vallortigara 1986a, 1986b, 1987a). Stereokinetic effects occur when certain 2-D patterns are rigidly rotated in the plane perpendicular to the line of sight. For instance, when a disc, with an eccentric dot on its surface, is slowly (between 5 and 20 revolutions per minute) rotated in the frontoparallel plane, after a short delay subjects report seeing a solid 3-D cone that has all the characteristic features of a real object (Bressan and Vallortigara 1987b).

There is evidence that non-human animals can extract structure from motion in the classical kinetic-depth displays of Wallach and O’Connell (1953), or in more recent computer-generated versions of them (for example, in primates, see Siegel and Andersen 1988; Perrett et al 1990). For instance, Cook and Katz (1999) trained pigeons to discriminate between computer-generated projections of cube and pyramid objects. The authors found that pigeons showed evidence of being able to recognise the structure of these objects from the pattern of their motion and were sometimes better at discriminating when all contour and surface information had been removed (eg with 2-D monochromatic coloured blobs moving consistently with the rigid projective geometry of either a cube or a pyramid).

However, stereokinetic phenomena are different from traditional structure-from-motion displays, in that the 2-D image is rotated rigidly in the frontal plane rather than deforming as a result of projective transformations. As far as we know, nobody
has yet investigated whether non-human species perceive the stereokinetic illusion (the only non-verbal beings in which the effect has been documented are human infants—Schmuckler and Proffitt 1994).

Vision is the primary sensory modality through which many animal species gather information about the surrounding world. The domestic chicken is one such species; in fact its behaviour depends strongly on visual modality, and it is for this reason considered an excellent model for investigating the structuring of visual space (see Vallortigara 2004a, 2004b).

Young domestic chicks succeed in many complex visual-perception tasks. It is known that humans perform perceptual completion of surfaces that are not present in the physical distribution of luminance, but are nevertheless ‘quasi-perceptive’, bringing about the perception of so-called ‘subjective contours’ (Kanizsa 1979). The first demonstration in a non-human species of subjective-contour perception was in fact obtained in the domestic chick (Zanforlin 1981; and see Nieder and Wagner 1999 for more recent evidence in other bird species, also complemented by neurophysiological data). Formation of illusory contours has been shown in the hens in the context of the perception of pictorial information (Forkman 1998). Using this paradigm, the animals must establish the direction of depth stratification, ie which surface is in front and which is behind, in chromatically homogeneous surfaces (Forkman and Vallortigara 1999).

One advantage provided by the young of this precocial species is that filial imprinting can be used as a tool for investigating basic perceptual mechanisms. Filial imprinting is the process whereby young birds learn to recognise the first conspicuous object they see after hatching (Lorenz 1935; Bateson 1966). Even after short exposure to an object (usually the mother hen, but artificial objects are just as successful) the chick develops a strong attachment to it. After imprinting occurs, the chick will approach and follow the object’s movement and will systematically avoid other, even very similar, objects. Imprinting can be used to some extent, as an equivalent of the techniques in use in developmental psychology to investigate perceptual and cognitive phenomena in prelinguistic children (Spelke 1998a, 1998b). For instance, Regolin and Vallortigara (1995) first demonstrated that 3-day-old chicks could show ‘amodal completion’ of partly occluded objects (see also Regolin et al 2004). Newborn chicks were reared singly with a red cardboard triangle, to which they rapidly imprinted and therefore regarded it as a social partner. Then the chicks were presented with pairs of stimuli composed of either isolated fragments or occluded parts of the imprinting stimulus. Chicks consistently chose to associate with complete or with partly occluded versions of the imprinting stimulus rather than with separate fragments of it. Moreover, chicks reared with a partly occluded triangle chose to associate with a complete triangle rather than with a fragmented one. However, chicks reared with a fragmented triangle chose to associate with a fragmented triangle and not with a complete one. Newly hatched chicks thus appear to behave as if they experienced amodal completion. These results were subsequently confirmed by Lea et al (1996), who also provided a direct comparison between newborn chicks and human infants. Regolin et al (2000) and Vallortigara et al (2005) recently used the imprinting method to investigate perception of biological motion in newly hatched chicks.

Here we used the imprinting paradigm to check whether young domestic chicks can perceive stereokinetic phenomena.

2 Experiment 1
In the first experiment we investigated the ability of chicks to perceive the stereokinetic cone effect (Musatti 1924). Animals of the experimental group were exposed to a pattern that appeared as a cone illusion to a human observer, and subsequently were required to choose between two solid objects: a solid 3-D cone constructed in order
to reproduce the illusory one and a cylinder of identical volume. Chicks of the control group (not imprinted) underwent a spontaneous free-choice test between the same two solid objects.

2.1 Method

2.1.1 Subjects. Subjects were 273 Hybro domestic chicks (\textit{Gallus gallus}). For the experimental group 89 female and 75 male chicks were used; for the control experiment 48 male and 61 female chicks were used. All chicks came from eggs that had been incubated in the dark for at least the last 7 days of incubation (ie from day 15 to day 21) and then hatched in our laboratory under controlled conditions. The fertilised eggs were delivered weekly to our laboratory from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza, Italy). Eggs were incubated till day 19 in standard conditions (temperature 37.5°C; humidity 55%–60%), and the chicks were then placed in a hatchery. The incubator, the hatchery, and the hatching room were all kept completely dark. This prevented the embryos from having any visual experience from the third week of incubation until they underwent the experimental procedure.

Such strict control placed on light exposure of the embryos and the newborn chicks is a standard procedure in these types of experiments (see for example Vallortigara et al 2005). The reason for this experimental design is that light exposure of the eggs in the last phase of incubation has been shown to affect the neural development and behaviour of chicks (see Rogers and Bolden 1991; Rogers et al 2004), and to create the most successful imprinting of the young birds onto the experimental stimuli. Moreover, as regards the control group, in order to assess spontaneous preferences of the chicks, it was necessary to exclude the occurrence of pre-exposure to any sort of visual stimuli.

2.1.2 Imprinting and test stimuli. The imprinting stimuli were 2-D orange cardboard discs (5 cm in diameter), similar to those employed by Musatti in his original research (1924, 1928, 1955, 1975). The orange colour was chosen in order to make the stimuli most attractive to newly hatched chicks (Hess 1956). We used two types of stimuli, the first of these was the simplest configuration that produced the stereokinetic cone illusion in human beings: a disc with a single eccentric black dot (0.2 cm in diameter, 1.5 cm from the disc centre) on its surface (figure 1a and movie file 1a). The second stimulus had three concentric black rings drawn on it, 2, 3, and 4 cm in diameter, 0.9, 0.6, and 0.3 cm, respectively, from the centre of the whole disc (figure 1b and movie file 1b). Such stimuli usually produce a more compelling 3-D effect in humans, than the previously described simpler disc (Zanforlin 1988a). The test stimuli consisted of

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{stimuli.png}
\caption{Stimuli producing the stereokinetic cone illusion: (a) an orange circle with a black eccentric dot; (b) an orange circle with concentric rings. (c) The two solid objects presented to the chick at test, the cone is a solid version of the stereokinetic cone (according to the formula by Zanforlin 1988a), the solid cylinder is a same-volume comparison.}
\end{figure}

\footnote{Note: Movie files can be seen on the \textit{Perception} website: http://www.perceptionweb.com/misc/p5420/}
two solid objects: a cone and a cylinder made of the same material and colour as the 2-D discs, with a dot identical to the eccentric one drawn in the appropriate position on the solid objects (figure 1c). The solid cone had a 5 cm diameter base and its height was estimated by expert observers (eight subjects, five males and three females, all experienced vision researchers) with normal or corrected-to-normal eyesight (for more details on the use of such procedure see Robinson et al 1985; Wilson et al 1986). The human observers were taken into the same room and also stood in front of the apparatus that was used for the chicks (70 cm from the stimuli). Each of the two 2-D stimuli was employed in turn, and the subjects were required to estimate the height of the stereokinetic illusion of the solid object they perceived. On the basis of the results, the height was set at 6.5 cm [the same result would be obtained by computing the height of the stereokinetic cone according to the model of Zanforlin (1987, 1988b)].

A cylinder with the same base dimension (5 cm) and volume (42 cm$^3$) of the cone, but of a different height (2.2 cm) was used as a comparison, since its perceptual characteristics, especially if observed from above, are largely similar to the stimulus used during imprinting.

2.1.3 Apparatus for imprinting. Chicks were housed in four boxes (6 cm $\times$ 6 cm) located in the hatchery room. The room was dark, except for two 60 W lamps that uniformly illuminated the imprinting stimuli (figure 2). The front of each box that housed the chicks was made of a transparent glass sheet. One single rotating stimulus was placed 22 cm away. This distance is sufficient to allow for binocular vision. The centre of the disc was approximately coaxial with the chick's eyes (4 cm from the floor). The rate of rotation of the disc was set at 8 revolutions per minute. To humans, such a stimulus looks like a solid cone. When viewed from the frontal plane, the base of the cone lies on the disc surface, and the apex points either towards or away from the observer.

2.1.4 Test apparatus. The apparatus consisted of a runway (72 cm $\times$ 20 cm $\times$ 30 cm) with two solid upright objects placed at each end. A pilot experiment has shown that vertically placed objects are more effective than the same objects placed horizontally in triggering the approach behaviour of chicks, perhaps because in this position the objects were better visually distinguishable. The runway was virtually subdivided into a central area (15 cm wide) and two side areas (each 28 cm long; figure 3). Each stimulus was illuminated by a 40 W lamp, while the rest of the room was completely dark. The chick was positioned in the central compartment and its behaviour was observed: chicks that remained in the central area for the duration of the experiment were classified as not having shown a preference for either object; chicks that did not remain in the central area showed a preference for one of the objects.
2.1.5 Procedure. At 1 or 2 days of age, a permanent marker was used to identify each of the chicks. The chicks were then exposed to the imprinting apparatus (a single rotating disc) for 4 h as shown in figure 2: 52 chicks were exposed to the simpler stimulus (figure 1a) and 112 to the more complex stimulus (figure 1b). At the end of the exposure, each chick was placed back in the hatchery in total darkness to avoid any further visual experience and to allow for memory consolidation (it is known that chicks’ affiliative behaviour is enhanced after a period in the dark as compared to chicks tested immediately after exposure—Johnson and Horn 1988).

Chicks of the control group were visually naive, ie they remained in the hatchery in total darkness until the test. Both control and experimental chicks were tested on day 3 after hatching (owing to yolk reserves, chicks can survive without food for the first 3 days after hatching—Hogan 1973), and with an identical procedure. The two solid stimuli were the very first objects seen by the control chicks, so that a spontaneous preference for either object could be assessed. On day 3, each chick was carried, in a closed small cardboard box, to the experimental room (located near the hatchery; temperature 29–30°C, humidity 68%), they were then placed in the central area of the test apparatus. Chick position at the starting point as well as the position of the two objects were balanced across animals. Chick’s behaviour was observed for a total of 6 min. A computer-driven event recorder allowed the experimenter to record the time spent by the chick in each of the three areas. The time spent by the chick near each object and the proportion of time spent by the solid cone was computed as \[
\frac{\text{time by the cone}}{\text{time by the cone} + \text{time by the cylinder}} \times 100.
\]
The index values range from 0 (full choice of the novel stimulus) to 100 (full choice of the imprinting stimulus). Significant departures from chance level (a score of 50) were estimated by one-sample two-tailed \(t\)-tests (see Vallortigara and Andrew 1991 for details of analyses).

Chicks’ preferences were analysed by analysis of variance (ANOVA) with sex (males versus females), object (the two different rotating discs shown in figure 1), day of imprinting as a between-subjects factor, and time (1 to 6 minutes) as a within-subjects factor.

Since chicks coming from modern commercial hatcheries have been largely subjected to artificial selection and not all individuals imprint easily, we excluded chick data from the analysis when imprinting did not occur (ie individuals spent all the time in the central area).

2.2 Results
Results for chicks in the experimental group are shown in figure 4. The ANOVA ran on the choices of the imprinted chicks showed that the main effects of sex, object, and day of imprinting were not statistically significant (all \(F_s < 1\)). Also their interactions were not significant (all \(F_s < 1\), except for the non-significant interaction...
Only the effect of time was significant ($F_{5,156} = 3.034$, $p < 0.05$), suggesting that choice became clearest in the last minutes of the test (see figure 4). There were no significant interactions involving time (all $Fs < 1$ except for time $\times$ day: $F_{5,156} = 1.097$, $p = 0.355$, ns; time $\times$ day $\times$ object: $F_{5,156} = 1.070$, $p = 0.367$, ns), apart for a marginal three-way interaction (time $\times$ sex $\times$ day: $F_{5,156} = 2.685$, $p < 0.05$). Therefore data were collapsed across sex, object, and day (figure 4a). Overall, in the 6-min test chicks preferentially approached and stayed closer to the cone (mean $\pm$ SEM $= 54.78 \pm 1.97$, one-sample $t$-test: $t_{163} = 2.43$, $p = 0.016$).

As shown in figure 4a, such preference appeared after the 2nd minute and became particularly clear in the last 2 minutes (5th minute: mean $\pm$ SEM $= 58.76 \pm 3.204$; $t_{163} = 2.733$, $p = 0.007$; 6th minute: mean $\pm$ SEM $= 57.47 \pm 3.351$; $t_{163} = 2.229$, $p = 0.027$).

The ANOVA on the time spent in the central area showed a progressive decrease in the time spent in the centre of the apparatus during testing ($F_{5,160} = 136.26$, $p < 0.001$; figure 4b). Such an effect is expected in this sort of test (Vallortigara and Andrew 1991), probably reflecting initial freezing of responses after placement in the apparatus and subsequent chick habituation to the novel environment.

Control chicks did not exhibit any spontaneous preferences for a particular object (see figure 5); the cone and the cylinder were similarly approached by naive chicks (mean $\pm$ SEM $= 47.96 \pm 1.56$; $t_{108} = -1.305$, $p = 0.19$). The ANOVA for the spontaneous choices of non-imprinted chicks (control group) did not reveal any statistically significant effects (all $Fs < 1$, except for time $\times$ sex: $F_{5,107} = 1.309$, $p = 0.270$, ns).

### 3 Experiment 2

In this experiment we exposed a novel group of chicks to a 2-D stimulus producing (to human beings) the illusion of a stereokinetic cylinder rather than a cone. Chicks were then required to choose, as in experiment 1, between a solid cylinder and a solid cone.

#### 3.1 Method

**3.1.1 Subjects.** Subjects were 126 Hybro domestic chicks (*Gallus gallus*), 67 males and 59 females. All chicks were hatched in our laboratory under controlled conditions.
and maintained in total darkness until the test, which took place on the 3rd day of life, as in experiment 1.

3.1.2 Apparatus. The apparatus for the imprinting and for the test were identical to those described in experiment 1.

3.1.3 Imprinting stimulus. The imprinting stimulus was made of two partially overlapping orange discs (each 5 cm in diameter, identical to the disc producing the stereokinetic cone illusion), so that the distance between the two centres was 0.8 cm (figure 6 and movie file). To humans such stimulus, when set in slow rotation, produces the perception of a stereokinetic cylinder (Zanforlin and Vallortigara 1988). We determined the size of the 2-D stimulus by using experienced human observers.

![Figure 6. The 2-D stimulus used in experiment 2 to produce the illusion of a stereokinetic cylinder.](image)

The same eight subjects (five males and three females) who judged the height of the stereokinetic cone in experiment 1 were required to choose, in a set of stereokinetic cylinder stimuli in which the distance between the centres of the two overlapping discs could be either 4, 6, 8, 10, or 12 mm, which stimulus best produced a solid cylinder 2.2 cm in height (ie the same solid 3-D object as that used in experiment 1). The subject was located in front of each of the stimuli (at a distance of 70 cm) and required to indicate which stimulus produced the impression of a cylinder most similar to the solid one, that was located, vertically, by the stereokinetic rotating stimulus. The subjects could see all the stimuli (presented one after the other in randomised sequence) repeated as many times as they liked. Five out of eight subjects chose the 8 mm stimulus as best representing the solid cylinder, one subject chose the 1 mm stimulus, and two subjects chose the 10 mm stimulus. We therefore decided to use in experiment 2 the stimulus in which the distance between the centres of the two overlapping discs was 8 mm (see figure 6).

3.1.4 Procedure. At 1 or 2 days of age each chick was singly taken from the hatchery and placed in the imprinting apparatus where it was exposed for 4 h to the rotating 2-D pattern of figure 6. At the end of the exposure, each chick was placed back in the hatchery in total darkness. The test procedure was the same as in experiment 1.

3.2 Results

The results are shown in figure 7. The ANOVA did not reveal any statistically significant effects (all Fs < 1). An analysis of the overall choice over the 6 minutes of testing revealed a significant preference for the cylinder stimulus (mean ± SEM = 53.99 ± 1.98, \( t_{121} = 2.01, p < 0.05 \); figure 7a).

The ANOVA on the time spent in the central area showed a progressive decrease in the time spent in the centre of the apparatus during testing, as in the previous experiment (\( F_{5,120} = 90.586, p < 0.001 \); figure 7b).
4 Discussion

The aim of this research was to provide the first investigation of the ability of animals to perceive stereokinetic illusions. The results of experiment 1 showed that chicks that had been exposed to a rotating disc approached the 3-D object most resembling the stereokinetic illusion. This outcome cannot be explained by a spontaneous preference for such an object, because the control experiment showed that naive chicks (not imprinted) were equally attracted to either of the two test objects. Moreover, in experiment 2, where the cylinder was used as the stereokinetic stimulus, chicks preferred the 3-D cylinder to the 3-D cone.

The pattern of 2-D stimulation available during imprinting (ie concentric circles) matched the frontoparallel projections of both a cylinder and a cone; therefore there was no possibility of choice at test based on a simple evaluation of similarity between imprinting and test stimuli in the absence of stereokinetic transformation. On the other hand, a cone and a cylinder seen in vertical position have very different 2-D projections (triangular- and rectangular-shaped, respectively) from that of the imprinting stimulus (circle-shaped). Thus, it seems likely that the chicks’ preferences emerged as a result of the stereokinetic transformation, ie as a result of the fact that the 2-D moving pattern seen during exposure (imprinting) did elicit the perception of a solid 3-D object.

It is quite plausible that, in spite of considerable differences in neuroanatomy (see, eg, Nguyen et al 2004), the avian and the mammalian visual system evolved the capacity of structuring space and object perception in a similar fashion. A large proportion of neurons in the optic tectum of birds is motion-sensitive, with a centre–surround organisation that allows the visual system of birds to be selective for relative motion (Frost and DiFranco 1976). In order to construct the structure of the surrounding space from the moving retinal input, birds also need the ability to extract the 3-D structure of the world. Little is known of the brain areas that may be involved in structure-from-motion perception in birds (though the caudal ectostriatum seems to be a plausible candidate—see Nguyen et al 2004). As to stereokinetic effects, current theories (Zanforlin 1988a, 1988b) suggest that the continuous flow of retinal projections produced by these patterns may simulate the conditions in the optic-flow tract that underlie extraction of structure from motion. The information in the optic-flow tract is in fact a reliable source for checking the relative velocity and the direction of movement and there is good evidence that birds possess the neurological apparatus to respond to optic-flow variations (for a review, see Frost and Sun 1997).

The fact that birds (at least one species of birds) seem to be susceptible to stereokinetic illusions suggests that the basic mechanisms involved in extracting structure from motion could be the same in the avian and mammalian brain. More experimental
work, with other bird species, is warranted in order to achieve a better understanding of these phenomena.

Acknowledgments. The experiments comply with the current Italian and European Community laws for the ethical treatment of animals. We wish to thank Giuseppe Clara for the design and construction of the apparatus, Elena Mascalzoni for the invaluable help provided with chick testing and care, and Paola Bressan for reading the manuscript and providing helpful comments.

References
Bateson P P G, 1966 “The characteristics and context of imprinting” Biological Reviews 41 177 – 220
Bressan P, Vallortigara G, 1986a “Subjective contours can produce stereokinetic effects” Perception 15 409 – 412
Bressan P, Vallortigara G, 1986b “Multiple 3-D interpretations in a classic stereokinetic effect” Perception 15 405 – 408
Forkman B, 1998 “Hens use occlusion to judge depth in a two-dimensional picture” Perception 27 861 – 867
Frost B J, DiFranco C E, 1976 “Motion characteristics of single units in the pigeon optic tectum” Vision Research 16 1229 – 1234
Hess E H, 1956 “Natural preferences of chicks and ducklings for objects of different colours” Psychological Reports 2 477 – 483
Musatti C L, 1924 “Sui fenomeni stereocinetici” Archivio Italiano di Psicologia 3 105 – 120
Musatti C L, 1928 “Sui movimenti apparenti dovuti ad illusione di identità di figura” Archivio Italiano di Psicologia 6 205 – 219
Musatti C L, 1955 “La stereocinesi e il problema della struttura dello spazio visibile” Rivista di Psicologia 49 3 – 57
Nieder A, Wagner H, 1999 “Perception and neuronal coding of subjective contours in the owl” Nature Neuroscience 2 660 – 663
Regolin L, Vallortigara G, 1995 “Perception of partly occluded objects by young chicks” Perception & Psychophysics 57 971 – 976