Are You as fooled as I am?

Visual Illusions in Human *(Homo)* and Nonhuman (*Sapajus, Gorilla, Pan, Pongo*) Primate Species

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Abstract

It has been argued that humans' susceptibility to visual illusions does not simply reflect cognitive flaws but rather specific functional adaptations of our perceptual system. The data on cross-cultural differences in the perception of geometric illusions seemingly support this explanation. Little is known, however, about the developmental trajectories of such adaptations in humans, let alone a conclusive picture of the illusionary susceptibility in other primate species. So far, most developmental or comparative studies have tested single illusions with varying procedural implementations. The current study aims at overcoming these limitations by testing human subjects of four different age classes (3- to 5 year-old children and adults) and five non-human primate species (capuchin monkeys, bonobos, chimpanzees, gorillas and orangutans) with an identical setup in five well-known geometric illusions (Horizontal-vertical, Ebbinghaus, Mueller-Lyer, Ponzo, Sander). Two food items of identical size were presented on separate trays with surrounding paintings eliciting the illusion of size differences and subjects were required to choose one of the items. Four of the five illusions elicited a strong effect in adult humans, and older children showed a greater susceptibility to illusions than younger ones. In contrast, only two illusions (Ebbingaus and Horizontal-vertical) elicited a mild effect on nonhuman primates with high variation within species and little variation between species. Our results suggests that humans learn to see illusions as they develop during childhood. They also suggest that future work should address how nonhuman primates' experience of these illusion changes throughout their development.

Introduction

Geometric illusions – broadly defined as misperceptions of a target object elicited by the contextual characteristics in which it is presented such that it looks larger, smaller, longer, shorter, or different along some other physical dimension (Feng et al., 2017) – have fascinated humans since their discovery. What strikes us most is their *cognitive impenetrability* (Pylyshyn, 1999) – the fact that the illusionary effect persists even when we explicitly know that our system is being "tricked". This apparent prevalence of perceptual over conceptual knowledge is not surprising, as perception must work quickly and frugally. Survival might depend on adequate immediate behavioral reactions to perceptual input, while conceptual decisions can be much more elaborate and can take much longer (Gregory, 1997).

At first glance, visual perception seems very basic and universality at least among humans might be expected (Fodor, 1983). However, in their pioneering studies Segall and colleagues tested 15 different human populations with different cultural and ecological backgrounds and found remarkable differences with respect to their susceptibility to visual illusions (Campbell et al., 1966; Segall et al., 1963a). Since then, several other studies have demonstrated cultural variation with respect to the effectiveness of geometric illusions. De Fockert and his team (2007) for example presented two versions of the Ebbinghaus illusion to Himba people in Namibia, a culture that is described as having no words for geometric shapes. Overall, the Himba showed less susceptibility to the illusion compared to urban western (British) participants. However, the authors argued that not the lesser naming abilities but rather their tendency to prioritize local over global feature analyses induced the differences observed in the accuracy of size judgements.

Several other cross-cultural studies also suggest that human populations with an increased holistic (global) mode of visual perception are typically more affected by illusionary effects (Berry, 1968, 1971; Dawson, 1967; Witkin, 1967) than humans who are preferentially locally oriented (e.g., Dakin & Frith, 2005; de Fockert et al., 2007; Happé, 1996; Happé et al., 2001). Those findings are not surprising, as one precondition for any geometric illusion to work is that the visual scene evoking the illusion must be perceived holistically. In other words, only if *global* features are preferentially analyzed at the expense of *local* features can susceptibility to an illusion be expected (Parron & Fagot, 2007).

Interestingly, a prevalence of global over local feature processing – the so-called *global precedence effect* (Navon, 1977) – that was shown in (western) humans could not be found in baboons (Fagot & Deruelle, 1997). Data from capuchin monkeys also suggests a more locally oriented processing style (Spinozzi et al., 2006; Truppa et al., 2017; Truppa et al., 2016). Whereas these monkey subjects primarily process the local features of a stimulus array, chimpanzees seem to fall in between humans and monkeys depending on the presentation format used. Chimpanzee subjects showed an advantage for processing local over global features in low-density conditions but no differences in dense conditions (Fagot & Tomonaga, 1999). Hopkins and Washburn (2002) tested rhesus monkeys and chimpanzees and showed that both species could discriminate between stimuli on the basis of their global configuration or on the basis of local elements. However, only the chimpanzees exhibited a global-to-local processing hierarchy, whereas the monkeys exhibited a local-to-global processing strategy, again suggesting a phylogenetic trend within the primate lineage (Fagot & Tomonaga, 1999).

Despite some empirical indications of a rather locally oriented processing style in some monkey species, their susceptibility to various visual illusions has been demonstrated for several populations. The following examples are chosen because of their special importance to the current study. Rhesus macaques were found to be susceptible to the Ponzo (Bayne & Davis, 1983; Fujita, 1997), the Mueller-Lyer (Tudusciuc & Nieder, 2010), the Zöllner (Agrillo et al., 2014b), the Horizontal-vertical (Dominguez, 1954), and the Duncker illusion (Zivotofsky et al., 2005). Capuchin monkeys perceived the Mueller-Lyer (Suganuma et al., 2007) and the Horizontal-vertical illusion (Dominguez, 1954), baboons perceived the Zöllner and corridor illusion (Barbet & Fagot, 2002; Benhar & Samuel, 1982), mangabeys and stumptail macaques were susceptible to the Horizontal-vertical illusion (Dominguez, 1954; Harris, 1966). Chimpanzees, the only ape species tested so far, were susceptible to the corridor illusion – a visually similar variant of the Ponzo illusion (Imura et al., 2008) – and the Delboeuf illusion – a variant of the Ebbinghaus illusion (Parrish & Beran, 2014b).

Besides primates, other mammalian species have been shown to be susceptible to geometric illusions too – for example in cats (Banszegi et al., 2021; Szenczi et al., 2019), dogs (Byosiere et al., 2020; Keep et al., 2018), and horses (Cappellato et al., 2020).

More than 90 years ago the effect of the Mueller-Lyer illusion and the Horizontal-vertical illusion was first demonstrated in birds, namely in ring doves (Warden & Baar, 1929), in chicks (Winslow, 1933) and more recently also for the famous grey parrot Alex (Pepperberg et al., 2008). The Ebbinghaus illusion also induced a strong effect in pigeons and domestic chicks – surprisingly, however, the illusionary effect was inverted compared to human subjects (Nakamura et al., 2008, 2014; but see Salva et al., 2013 for different results). Even phylogenetically quite distantly-related species such as reptiles (Santaca et al., 2019; Santaca, Petrazzini, Agrillo, et al., 2020; Santaca, Petrazzini, Wilkinson, et al., 2020) and fish (Agrillo et al., 2020; Fuss & Schluessel, 2017; Sovrano et al., 2016) seemed susceptible to the effects of some geometric illusions.

Visual illusions have also been the subject of interest in developmental psychology. For children below seven years of age, the accuracy of size discrimination seems to be affected much less by the surrounding context compared to adults. When confronted with the Ebbinghaus illusion, adults have problems distinguishing between two circles of different sizes until they differ by more than 10%, whereas children between four and six years of age reliably differentiate between two circles when the size difference is not more than 2% (Doherty et al., 2010). By ten years of age, context-sensitivity or illusionary susceptibility is still not at adult levels, which means that children literally see the world more correctly than they will as adults.

Despite several examples of illusionary effects in different species and taxa, the general picture resulting from several animal studies remains inconclusive, with evidence for and against susceptibility to visual illusions. Additional complication arises from the fact that the experimental methodology used in the different studies, rather than the predominant processing style (local/global) *per se*, may have favored one processing style over the other (Parrish et al., 2015) and therefore facilitated or diminished potential illusionary effects in the subjects (for a related discussion see also Santaca et al., 2021). To the best of our knowledge, the vast majority of studies that investigated illusionary effects in human as well as non-human subjects used various forms of computerized settings (e.g., matching-to-sample procedure) or other procedures that require extensive training before the actual testing takes place (e.g., Agrillo et al., 2014a; Nakamura et al., 2008; Parrish et al., 2015; Suganuma et al., 2007). Computerized setups allow for a very precise control of the independent variables but at the same time lose some ecological validity due to their artificial nature and the massive amount of training required prior to the test.

In the current study, we used a paradigm that rendered extensive prior training unnecessary as the inherent logic of the task was completely intuitive and straightforward. Food items served as test stimuli and subjects simply had to indicate (point to) the stimulus they wanted to receive (for a similar approach see Parrish & Beran, 2014a; Petrazzini et al., 2017; Santaca et al., 2019; Szenczi et al., 2019). The underlying assumption was that if one of two stimuli (food items) appeared larger than the other, the subject should preferentially choose that one in order to maximize its caloric intake. Control conditions explicitly served to validate this assumption by giving subjects the choice between non-illusionary stimuli of objectively different sizes.

A unique feature of the current study is the diversity and scope of the study population, which includes five non-human primate species – four closely related great ape (bonobos, chimpanzees, gorillas, orangutans) plus one rather distantly related monkey species (capuchins) – and four different human samples (3y, 4y, 5y, adults), all of which were systematically tested on the same five geometric illusions.

Experiment 1 – Humans

Method

Subjects

We tested 26 adults (13 women, *mean* age = 24.9 y, *SD* = 1.37), 26 three-year-old children (13 girls, *mean* age = 3.45 y, *SD* = .34), 25 four-year-old children (12 girls, *mean* age = 4.42 y, *SD* = .29) and 23 five-year-old children (12 girls, *mean* age = 5.46 y, *SD* = .30). All participants had normal or corrected-to-normal vision and were predominantly white, middle-class and came from a medium-sized Canadian university city, where they were already recruited to participate in another psychological study. The research with children was approved by the Office of Research Ethics and Integrity at the University of Ottawa. Parents of the children provided written informed consent for their children's participation. Children also provided their verbal assent.

Material

Test stimuli were pretzel sticks and bread wafers presented on two separate gray plastic boards with notches in which the food items were placed. In the illusion conditions, the two boards differed with respect to the paintings surrounding the notches, with each painting evoking the respective illusion within a given pair (see Figure 1). In the control conditions, subjects could choose between an objectively small food item and a big item without any surrounding paintings.

The stimuli boards were presented next to each other on a table with a 45-degree incline. The stimuli for the "stick illusions" (pretzel sticks) were 5 mm thick and between 60 and 120 mm long (Ponzo = 60 mm, Mueller-Lyer = 80 mm, Horizontal-vertical = 100 mm, Sander = 120 mm). The stimuli for the Ebbinghaus illusion (bread wafers) were 64 mm in diameter and 2 mm thick. Whereas the objective size of the two food items within each illusion condition was identical, the food items in the control conditions objectively differed in size by a factor of 1.7 for Stick Control 1 (big = 100 mm vs. small = 60 mm length) and by a factor of 3.3 for Circle Control (big = 64 mm vs. small = 35 mm DM).

Procedure

Children were presented with seven conditions: five geometrical illusions (Horizontal-vertical, Ebbinghaus, Mueller-Lyer, Ponzo, Sander) and two control conditions (Stick Control, Circle Control). All participants received 14 trials (two trials per condition) in a randomized fashion, counterbalanced so that each illusionary stimulus appeared left and right once and both trials of one condition never appeared in succession.

At the beginning of the session, experimenter (E) explained to the child that they would be playing a game collecting stickers. Next E said: "*I am going to ask you some questions and every time you answer one of my questions you can take one sticker from the sticker book and stick it on your paper*". For each trial, E took two boards out of a drawer and placed the food items inside the notches. While the stimuli were still facing away from the child, E asked "*Ready?*". Then, E turned around both boards simultaneously, so that the child could see both stimuli next to each other. Next, E asked the following question: "*Is one of the two pretzels/cookies larger?*", and if the child answered "*Yes*", E continued by asking "*which one, can you point at it?*". In order to avoid any differential reinforcement, children received a sticker every time they answered the questions, regardless of which stimulus they pointed at.

Data scoring and analysis

Our dependent variable was the percentage of trials in which subjects selected the illusionary larger stimulus of a given pair (large chosen => score 1, small chosen => score 0). If the stimuli presented did not induce any illusionary effect, the subject would be expected to choose indifferently between the two boards (chance level average = 0.5). Accordingly, if the child answered indifferently in a given trial (e.g., *"both items are the same size"*) we gave her a chance score (0.5). A second observer (CP) scored 10% of the sessions (= 140 trials) to assess inter-observer reliability. Inter-observer reliability was excellent (Cohen's kappa = 1).

We used exact Wilcoxon signed-rank tests (two-tailed) for each illusion to asses if the percentage of trials in which subjects selected the illusionary larger stimuli differed significantly from the chance level (50%). To analyze potential age effects, we fitted a generalized linear mixed model (GLMM; Baayen, 2008) with binomial error structure and log link function (McCullagh & Nelder 1989). The subjects' choice was included as a dependent variable, age class (an ordered factor) as fixed effect, and subject ID as a random effect. The model was fitted in R (version 3.5.0, R Core Team. 2018; package lme4 1.1-17; Bates, Mächler, Bolker & Walker, 2015).

As the two control conditions served as a baseline criterion to ensure that subjects actually preferred the larger food item when the two stimuli objectively differed in size, only subjects that chose the larger of the two stimuli in both trials of the respective control condition (2/2) were included in the statistical analyses for each illusion condition. Due to the Stick Control drop-out criterion, four children (two three-year-olds, two four-year-olds) were excluded from analyzing the Mueller-Lyer, Horizontal-vertical, Ponzo, and Sander data, resulting in a final sample size of 24 three-year-olds (12 girls), 23 four-year-olds (12 girls) and 23 five-year-olds (11 girls). Due to the Circle Control drop-out criterion, three children (one three-year-old, one four-year-old, one five-year-old) were excluded from analyzing the Ebbinghaus data, resulting in a final sample size of 25 three-year-olds (12 girls), 24 four-year-olds (12 girls) and 22 five-year-olds (11 girls). All 26 adults were included in the statistical analyses as there were no control drop-outs.

Standards for openness and transparency

We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Results

Ebbinghaus illusion

Subjects' susceptibility to the Ebbinghaus illusion was significantly influenced by their age ($X^2 = 43.68$, $df = 3$, $p < 0.001$, see Figure 2). The older the subjects, the more they preferred the illusionary larger stimulus. Adult subjects preferentially chose the illusionary larger item ($mean_{large} = 92.3\%$) and their choice significantly differed from chance ($Z = -4.69$, $n = 26$, $p < 0.001$, effect size $r = 0.65$). Five-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than adults ($mean_{large} = 75.0\%$), and their choice significantly differed from chance ($Z = -2.84$, $n = 22$, $p = 0.007$, effect size r

= 0.43). Four-year-old children did not show a clear preference for the illusionary larger item ($mean_{large}$ = 58.3%) and their choice did not significantly differ from chance (Z = –1.07, n = 24, p = .42, effect size r = 0.15). Three-year-old children preferentially chose the illusionary smaller item ($mean_{large}$ = 30.0%) and therefore showed an opposite pattern compared to adults and five-year-olds. Their choice significantly differed from chance (Z = –2.50, n = 25, p = 0.021, effect size r = 0.35). Table 2 provides a summary of the performances for each age group tested.

Horizontal-vertical illusion

Subjects' susceptibility to the Horizontal-vertical illusion was significantly influenced by their age (X^2 = 15.06, df = 3, p = 0.002). The older the subjects, the more they preferred the illusionary larger stimulus. Adult subjects preferentially chose the illusionary larger item ($mean_{large}$ = 96.2%) and their choice significantly differed from chance (Z = –4.90, n = 26, p < 0.001, effect size r = 0.68). Five-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than adults ($mean_{large}$ = 89.1%), and their choice significantly differed from chance (Z = –4.24, n = 23, p < 0.001, effect size r = 0.63). Four-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than adults and five-year-olds ($mean_{large}$ = 78.3%), and their choice significantly differed from chance (Z = –3.15, n = 23, p = 0.002, effect size r = 0.46). Three-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than all other age groups ($mean_{large}$ =

70.8%), and their choice significantly differed from chance ($Z = –3.16$, $n = 24$, $p = 0.002$, effect size $r = 0.46$).

Mueller-Lyer illusion

There was a trend for subjects' susceptibility to the Mueller-Lyer illusion to be influenced by their age ($X^2 = 6.48$, $df = 3$, $p = 0.091$). The older the subjects, the more they preferred the illusionary larger stimulus. Adult subjects exclusively chose the illusionary larger item ($mean_{large} = 100\%$) and their choice significantly differed from chance ($Z = –5.10$, $n = 26$, $p < 0.001$, effect size $r = 0.71$). Five-year-old children also preferentially chose the illusionary larger item ($mean_{large}$ 97.8%) and their choice significantly differed from chance ($Z = –4.69$, $n = 23$, $p < 0.001$, effect size $r = 0.69$). Four-year-old children also preferentially chose the illusionary larger item ($mean_{large} = 95.7\%$) and their choice significantly differed from chance ($Z = –4.58$, $n = 23$, $p < 0.001$, effect size $r = 0.68$). Three-year-old children also preferentially chose the illusionary larger item ($mean_{large} = 91.7\%$) and their choice significantly differed from chance ($Z = –4.47$, $n = 24$, $p < 0.001$, effect size $r = 0.65$).

Sander illusion

Subjects' susceptibility to the Sander illusion was significantly influenced by their age ($X^2 = 17.26$, $df = 3$, $p = 0.001$). The older the subjects the more they preferred the illusionary larger stimulus. Adult subjects exclusively chose the illusionary larger item ($mean_{large} = 100\%$) and their choice significantly differed from chance ($Z = –5.10$, $n = 26$,

$p < 0.001$, effect size $r = 0.71$). Five-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than adults ($mean_{large}$ 89.1%), and their choice significantly differed from chance ($Z = -4.24$, $n = 23$, $p < 0.001$, effect size $r = 0.69$). Four-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than adults and five-year-olds ($mean_{large} = 78.3\%$), and their choice significantly differed from chance ($Z = -3.61$, $n = 24$, $p < 0.001$, effect size $r = 0.53$). Three-year-old children also preferentially chose the illusionary larger item, but to a lesser degree than all other age groups ($mean_{large} = 72.9\%$), and their choice significantly differed from chance ($Z = -3.05$, $n = 24$, $p = 0.003$, effect size $r = 0.44$).

Ponzo illusion

Adult subjects did not show a preference for the illusionary larger item ($mean_{large} = 59.6\%$) and their choice did not significantly differ from chance ($Z = -1.07$, $n = 24$, $p = .42$, two-tailed). Even though pilot data suggested otherwise, the illusionary effect obviously did not emerge during actual testing with the stimuli used. We therefore excluded the Ponzo illusion from further analyses of children’s as well as non-human primates’ data because the main assumption – that the stimuli clearly induce an illusion in human adults – did not seem justified.

Experiment 2 – Apes & Capuchins

Method

Subjects

We tested six bonobos (four females) with ages between 8 and 33 years (*mean* = 18.5, *SD* = 8.5), 17 chimpanzees (10 females) with ages between 7 and 41 years (*mean* = 26.9, *SD* = 12.9), six gorillas (two females) with ages between 3 and 29 years (*mean* = 11.5, *SD* = 6.3, seven orangutans (four females) with ages between 7 and 36 years (*mean* = 18.3, *SD* = 11.3), and eight tufted capuchin monkeys (four females) with ages between 10 and 26 years *(mean* = 15.0y, *SD* = 4.9). All bonobos, chimpanzees, orangutans and two gorillas were housed at the Wolfgang Köhler Primate Research Center in Leipzig Zoo, Germany. Four gorillas (males) were tested at Loro Park in Tenerife and all of the capuchin subjects were tested at the Primate Center of the Institute of Cognitive Sciences and Technologies (CNR) in Rome, Italy. All 45 subjects lived in social groups of various sizes, with access to indoor and outdoor areas. Prior to this experiment, the Leipzig and Rome subjects had participated in a number of cognitive studies that involved selecting one of two objects to get a reward. All subjects were individually tested in their indoor cages and were not deprived of food or water. The sample size was determined by the availability of ape and monkey subjects at the research facilities involved.

Materials

We used the exact same stimuli as those used with humans.

Procedure

Subjects (S) sat across from the experimenter (E), separated by a mesh panel or a Plexiglas window with three small holes at its bottom through which S could indicate their choices by pointing to the tray whose contents they wanted to receive. Subjects always received the content of the board they selected and were therefore never differentially reinforced (except for the control condition).

A trial started when E baited the stimuli boards while they were turned away from S. Once the food items were placed into their notches, E turned the stimuli boards around so that the front sides of the two boards were now visible to S (about 40-60 cm distance from S's eyes to stimulus). After S looked at the stimuli boards for 3-5 seconds, E moved the sliding table forward, thereby allowing S to choose one of the boards by pointing or touching (see figure 3 in supplemental material). The five different illusion pairs and the two control pairs were presented six times each in an intermixed and counterbalanced fashion, with the illusionary larger stimulus never appearing more than two times in a row on the same side (42 trials in total). Whenever S touched both sides simultaneously the trial was repeated. As soon as the subject clearly indicated one side, E fed that item through the middle hole. If subjects lost interest during presentation and left the testing station, the trial was cancelled and restarted. Inter-trial intervals were approximately 30-60 seconds for each condition, depending on individual participation and E's reloading speed.

Data scoring and analysis

All trials were videotaped. Our dependent variable was the percentage of trials in which subjects selected the illusionary larger stimulus of a given pair. The control conditions served as a baseline criterion to ensure that subjects actually preferred the larger food item when the two stimuli objectively differed in size. A second observer

(CP) scored 10% of the sessions (= 189 trials) to assess inter-observer reliability. Inter-observer reliability was excellent (Cohen's kappa = .94). As for the human sample, we used exact Wilcoxon signed-rank tests (two-tailed) for each illusion to asses if the percentage of trials in which subjects selected the illusionary larger stimuli significantly differ from the chance level (50%).

Even though pilot data suggested otherwise, only four of the stimuli pairs induced the intended illusionary effect in adult humans during the actual experiment (Ebbinghaus, Mueller-Lyer, Horizontal-vertical, Sander; see results of Experiment 1). We therefore excluded the Ponzo illusion from further analyses of non-human primates' data.

Only subjects that chose the larger of the two control stimuli in more than 80 percent of the cases (5/6 trials) were included in the statistical analyses. The following number of subjects were excluded from analyzing the "stick illusions" data (Mueller-Lyer, Horizontal-vertical, Ponzo, Sander) due to the Stick Control drop-out criterion: three chimpanzees, two orangutans, and two gorillas, resulting in a final sample size of 15 chimpanzees, four gorillas and five orangutans. The following number of subjects were excluded from analyzing the "circle illusion" data (Ebbinghaus) due to the Circle Control drop-out criterion: one chimpanzee and one gorilla, resulting in a final sample size of 16 chimpanzees, six gorillas and seven orangutans. All of the six bonobo and eight capuchin subjects met the criterion of both control conditions and were therefore included in all further analyses.

We used Kruskal–Wallis tests (two-tailed) for each illusion to asses if the percentage of trials in which subjects selected the illusionary larger stimuli differed significantly between species. We used Mann-Whitney tests (two-tailed) to analyze pairwise inter-specific differences. We used exact Wilcoxon signed-rank tests (two-tailed) for each illusion to asses if the percentage of trials in which subjects selected the illusionary larger stimuli differed significantly from chance level (50%).

Results

Ebbinghaus illusion

Subjects' susceptibility to the Ebbingaus illusion was not significantly influenced by species (Kruskal-Wallis test: $X^2 = 4.53$, $df = 4$, $n = 43$, $p = 0.34$, effect size $\eta^2 = 0.01$, see Figure 2). Therefore, we pooled together the data of all species in subsequent analyses. Subjects preferentially chose the illusionary larger item above chance levels (Wilcoxon test: $Z = –3.68$, $n = 43$, $p < 0.001$, effect size $r = 0.40$). For a summary of individual subjects' performances see Table 1 and for group level performance see Table 2 in the supplemental material).

Horizontal-vertical illusion

Subjects' susceptibility to the Horizontal-vertical illusion was not significantly influenced by species (Kruskal-Wallis test: $X^2 = 7.13$, $df = 4$, $n = 38$, $p = 0.13$, effect size $\eta^2 = 0.10$). Therefore, we pooled together the data of all species in subsequent analyses. Subjects preferentially chose the illusionary larger item above chance levels (Wilcoxon test: $Z = –2.53$, $n = 38$, $p = 0.011$, effect size $r = 0.29$).

Mueller-Lyer illusion

Subjects' susceptibility to the Mueller-Lyer illusion was significantly influenced by species (Kruskal-Wallis test: $X^2 = 9.90$, $df = 4$, $n = 38$, $p = 0.042$, effect size $\eta^2 = 0.18$). Pairwise comparisons revealed that capuchin monkeys were more likely to select the illusionary larger item than bonobos (Mann-Whitney test: $U = 7$, $n = 14$, $p = 0.029$), chimpanzees (Mann-Whitney test: $U = 26.5$, $n = 23$, $p = 0.028$) and orangutans (Mann-Whitney test: $U = 4$, $n = 13$, $p = 0.019$). However, none of the species selected the illusionary larger item above chance levels (Wilcoxon test: $Z > -2.0$, $p > 0.08$ in all cases, effect sizes $r = 0.19 - 0.52$, see Figure 2).

Sander illusion

Subjects' susceptibility to the Sander illusion was not significantly influenced by species (Kruskal-Wallis test: $X^2 = 4.86$, $df = 4$, $n = 38$, $p = 0.30$, effect size $\eta^2 = 0.03$). Therefore, we pooled together the data of all species in subsequent analyses. Subjects did not preferentially choose the illusionary larger item above chance levels (Wilcoxon test: $Z = -1.15$, $n = 38$, $p = 0.25$, effect size $r = 0.13$).

General Discussion

Four of the five initially presented illusions elicited a strong effect in adult humans. Children seemed to perceive the illusionary effect too but to a generally lesser degree, although their susceptibility steadily increased with age. In contrast, only two of the four illusions (Ebbingaus and Horizontal-vertical) elicited an illusionary effect on nonhuman primates, which was invariably weaker than the effect observed in humans. We found no conclusive evidence that the Mueller-Lyer or the Sander illusion caused illusionary effects in nonhuman primates. In addition, it is worth mentioning that while the variances within the human samples were rather low, the non-human samples showed high variation within and low variation between the individual species.

Within the human sample we found a clear developmental trajectory. Subjects' susceptibility to all four (finally included) illusions was significantly influenced by their age. The older the subjects the stronger their susceptibility, with adult humans showing the strongest and the youngest children the weakest illusionary effect. Such a developmental trend is consistent with previous reports that suggest a gradual transition from local to global processing style between the age of five and nine years (De Lillo et al., 2005; Neiworth et al., 2006; Poirel et al., 2008). To complete the picture, it needs to be mentioned though that newborn babies seem to show some kind of global preferences (Cassia et al., 2002), which might be explained by the fact that their perceptual system is yet physiologically too rudimentary to allow for a detailed visual processing of local elements. Coming from a cross-cultural perspective, McCauley and Henrich (2006) speculated that "[…] whatever causes the members of these different societies to vary in their susceptibility to the illusion likely has its effects between birth and age twenty […]". Other studies corroborate that claim by showing that context-sensitivity – a precondition for any illusionary effect – is positively correlated with mental age (Doherty et al., 2010). Such ontogenetic progress towards broader contextual synthesis in perception is generally advantageous for the individual but not when the context is misleading, as in the case of visual illusions. In other words, given misleading surroundings of a visual scene, young children might see the world more accurately than adults; our cognitive maturation seems to facilitate illusionary susceptibility. Interestingly, the current data not only showed that the youngest children (3y) were the ones with the least illusionary impact for three of the four illusions, but also revealed an inverse effect for one illusion (Ebbinghaus) – they overestimated the size of the stimulus that appeared smaller to older children and adult subjects. Future studies might investigate more explicitly whether or not the inverse Ebbinghaus effect observed in three-year-olds has actual cognitive underpinnings or was a procedural artefact of the current setup.

Our comparative results are largely consistent with the existing nonhuman primate literature. The Horizontal-Vertical illusion is the most commonly reported illusion in monkeys (Dominguez, 1954; Harris, 1966) and our data confirmed this finding in a sample mostly composed by apes. We also found an effect of the Ebbingaus illusion, which has been previously reported in chimpanzees implemented as the visually similar Delbouef illusion (Parrish & Beran, 2014b). In contrast, we did not find an effect for the Mueller-Lyer illusion even though it has been previously reported in rhesus macaques and capuchin monkeys (Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007; Tudusciuc & Nieder, 2010), but we found that capuchins were more susceptible to this illusion than apes. The most discrepant result in our sample was the Ponzo illusion which we failed to elicit despite being previously reported for rhesus macaques, baboons and chimpanzees (Bayne & Davis, 1983; Barbet & Fagot, 2002; Fujita, 1997; Imura, Tomonaga, & Yagi, 2008). Note, however, that our results of the Ponzo illusion should be interpreted cautiously because our materials also failed to elicit this illusion in humans.

The global-local processing style has been invoked as a potential explanation for the difference between humans and nonhumans in perceiving illusions. If we assume that nonhuman primates are less globally oriented than humans, an assumption that is supported by empirical evidence (Fagot & Deruelle, 1997; Fagot & Tomonaga, 1999), our results are consistent because humans, especially older children and adults, showed much stronger illusionary effects than any of the primate species. However, if we focus exclusively on nonhuman primates and assume that chimpanzees process stimuli more globally than monkeys, again something that has received some empirical support (Fagot & Deruelle, 1997; Hopkins & Washburn, 2002; Truppa, De Simone, & De Lillo, 2016), our data do not support the global-local precedence as an explanation for inter-specific differences. First of all, despite the putative differences in global-local processing between monkeys and apes, we found no significant differences between species in most tests. Second, and more revealing perhaps, is that in the only test showing inter-specific differences, capuchins were actually more susceptible to the Mueller-Lyer illusion than chimpanzees, bonobos or orangutans. This is precisely the opposite that one would predict based on the global-local processing modes of chimpanzees (apes) and capuchin (monkeys). However, we refrain from overinterpretation here, as neither the performances of the capuchins nor any of the ape species individually differed significantly from chance. Overall, the small non-human sample size presents a serious limitation of the current study as it may have prevented us from detecting significant differences in some conditions and species.

Given that our main focus was on primates, far-reaching inter-species comparisons are hard to make, among other things because of the different methodologies that have been used and the general diversity of perceptual systems of those species from which data exist. Nevertheless, it is worth mentioning that for some of these illusions the results previously obtained from non-primate species (mainly birds) paint a comparable picture of mostly weak to moderate effects (Fujita et al., 1991; Qadri & Cook, 2019). Some of those studies have investigated in great detail the determinants of illusory effects by varying experimental, spatial, and attentional factors (e.g., Qadri & Cook, 2015) – a level of analysis that the current study was not designed to address. On the contrary, the methodological conformity across tasks and species was an explicit goal to allow for meaningful comparisons.

The observed differences between human and the non-human susceptibility plus the described ontogenetic trajectory in children revive the question of potential explanations for geometric illusion in general. For one of the most extensively studied illusions in humans and the one that elicited the strongest effects in the current study – the Mueller-Lyer Illusion – an ecological explanation had been suggested. The so-called 'Carpentered World Hypothesis' claims that the housing conditions of human populations and their everyday exposure to rooms with right-angled corners determine their susceptibility to this illusion. When confronted with a two-dimensional image, our visual system automatically creates a three-dimensional representation in which the angle at the end of the lines induces a perception of depth (Gregory, 1966). As a result, viewers perceive the length of the two imbedded lines differently, implicitly "assuming" they indicate different positions in a three-dimensional space. Interpretations of this kind were given as an explanation for earlier studies that reported cross-cultural differences, namely that human populations that do not live in "carpentered" buildings are less (if at all) susceptible to this illusion (e.g., Segall et al., 1963b). It has been speculated additionally that exposure to perspective in art with three-dimensional paintings might also contribute to the emergence of illusionary effects that seem particularly pronounced in western societies (McCauley & Henrich, 2006).

Another aspect worth investigating more extensively is the interaction between peripheral and central mechanisms involved in visual illusions, an area of active debate in visual cognition research. Neurobiological studies have shown that, for example, intercortical interactions may affect perception of illusionary contours through “top-down” cortico-cortical feedback mechanisms in both humans (Seghier & Vuilleumier, 2006; Wokke et al., 2013) and non-human primates (Lee & Nguyen, 2001). Therefore, the emergence of illusionary percepts involves reverberation across multiple networks including secondary visual areas in primate species. Although these mechanisms are still far from being elucidated, it is plausible to hypothesize that differences in the functioning of networks involving secondary visual areas could partly account for age- and species-related differences reported here and in previous studies on primates.

Finally, given the observed developmental patterns in human subjects it seems essential to investigated potential age effects also in non-human subjects. Some studies suggest developmental effects in mammals (Banszegi et al., 2021) and birds (Rosa Salva et al., 2013) but unfortunately, the size of the current non-human primate sample does not allow for any meaningful analysis of this kind. Larger samples through multi-lab collaborations (e.g., ManyPrimates, 2019) and counterbalanced age compositions of the testing groups would allow for more controlled analyses of age effects in nonhuman subjects in the future.

There is consensus that visual illusions can be used to reveal the neural correlates underlying perception (Eagleman, 2001). Moreover, different types of illusions can be mediated by different neuronal populations (Song et al., 2011). The behavioral study of visual illusions combined with experimental techniques increasingly capable of measuring neural activity could contribute in the future to further disclose mechanisms underlying complex phenomena of visual (mis)perception in humans and nonhumans.

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Ethical statements

The study was ethically approved by an internal committee of the Max Planck Institute for Evolutionary Anthropology (director, research coordinator) and the Leipzig zoo (head keeper, curator, vet). No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. Research was non-invasive and strictly adhered to the legal requirements of Germany. Animal husbandry and research comply with the “EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria”, the “WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums” and the “Guidelines for the Treatment of Animals in Behavioral Research and Teaching” of the Association for the Study of Animal Behavior (ASAB). IAUCUC was not necessary to conduct this research. In accordance with the recommendations of the Weatherall report “The use of non-human primates in research” groups of apes were housed in semi-natural indoor and outdoor enclosures containing climbing structures, such as ropes and platforms; and natural features, such as vegetation, trees and streams. They received regular feedings, had access to enrichment devices including shaking boxes and poking bins, and water ad lib. Subjects voluntarily participated in the study and were never food or water deprived. Research was conducted in the sleeping and/or observation rooms.

The study on capuchin monkeys was approved by the Italian Health Ministry (Central Direction for the Veterinary Service, approvals n.11/2011-C and n.132/2014-C to V.Truppa).

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Table 1: Individual performance for all nonhuman subjects and species. Numbers represent mean proportion of trials (in %) in which subjects chose the illusionary larger stimulus for each of the four illusions.

Subject	Species	Sex	Age	Percentage of trials in which the illusionary larger stimulus was chosen			
				Ebbinghaus	**Hori-Verti**	**Mueller**	**Sander**
Fimi	Bonobo	f	8	67	67	0	67
Joey	Bonobo	m	33	83	83	50	0
Kuno	Bonobo	m	20	67	100	0	67
Lexi	Bonobo	f	17	67	83	67	17
Luiza	Bonobo	f	11	67	83	33	83
Yasa	Bonobo	f	24	67	100	50	33
Robot	Capuchin	m	17	100	67	67	33
Robin	Capuchin	m	15	100	67	67	33
Roberta	Capuchin	f	26	100	83	83	50
Robiola	Capuchin	f	15	100	83	67	67
Sandokan	Capuchin	m	13	17	83	83	100
Rucola	Capuchin	f	13	83	17	50	50
Quincy	Capuchin	f	10	17	50	83	67
Pedro	Capuchin	m	11	83	33	33	33
Alex	Chimp	m	15	0	100	17	67
Bangolo	Chimp	m	7	67	67	83	50
Dorien	Chimp	f	36	83	67	0	33
Fraukje	Chimp	f	40	33	50	50	33
Frederike	Chimp	f	42	83	X	X	X
Frodo	Chimp	m	23	100	67	33	50
Hope	Chimp	f	25	67	17	67	33
Kisha	Chimp	f	12	80	X	X	X
Kofi	Chimp	m	11	100	83	67	50
Lobo	Chimp	m	12	83	50	17	17
Lome	Chimp	m	15	100	83	67	43
Natasha	Chimp	f	36	X	17	50	50
Riet	Chimp	f	39	33	33	17	33
Robert	Chimp	m	41	50	17	50	33
Sandra	Chimp	f	23	100	50	50	50
Swela	Chimp	f	21	50	50	50	67
Tai	Chimp	f	14	67	50	50	33
Abeeku	Gorilla	m	17	67	X	X	X
Aladin	Gorilla	m	17	50	33	83	43
Diara	Gorilla	f	3	50	X	X	X
Kibara	Gorilla	f	12	83	50	50	43
Noel	Gorilla	m	29	67	100	50	67
Rafiki	Gorilla	m	24	67	83	50	83

Batak	Orang	m	7	83	X	X	X
Bimbo	Orang	m	36	67	33	33	17
Dokana	Orang	f	27	33	100	50	33
Padana	Orang	f	19	50	17	50	67
Pini	Orang	f	28	33	83	33	33
Suaq	Orang	m	7	67	X	X	X
Tanah	Orang	f	7	67	50	17	17

Table 2: Summary of performance for all human and nonhuman groups tested. Numbers represent mean proportion of trials (in %) in which the illusionary larger stimulus was chosen. Asterisks indicate significant difference from chance level with *p < 0.05, **p < 0.01, ***p < 0.001.

	Mean choice (%)	**Ebbinghaus**	**Horizontal-Vertical**	**Mueller-Lyer**	**Sander**
Humans	**Human adults**	92.3***	96.2***	100***	100***
	Human 5y	75.0**	89.1***	97.8***	89.1***
	Human 4y	58.3	78.3**	95.7***	78.3***
	Human 3y	*30.0**	70.8**	91.7***	72.9**
Non-Humans	**Bonobos**	69.4	86.1	33.3	44.4
	Capuchins	75.0	60.4	66.7	54.2
	Chimpanzees	68.5	53.3	44.4	42.9
	Gorillas	63.9	66.7	58.3	58.9
	Orangutans	57.1	56.7	36.7	33.3
	Non-humans (ALL)	67.4***	61.8*	47.8	45.9

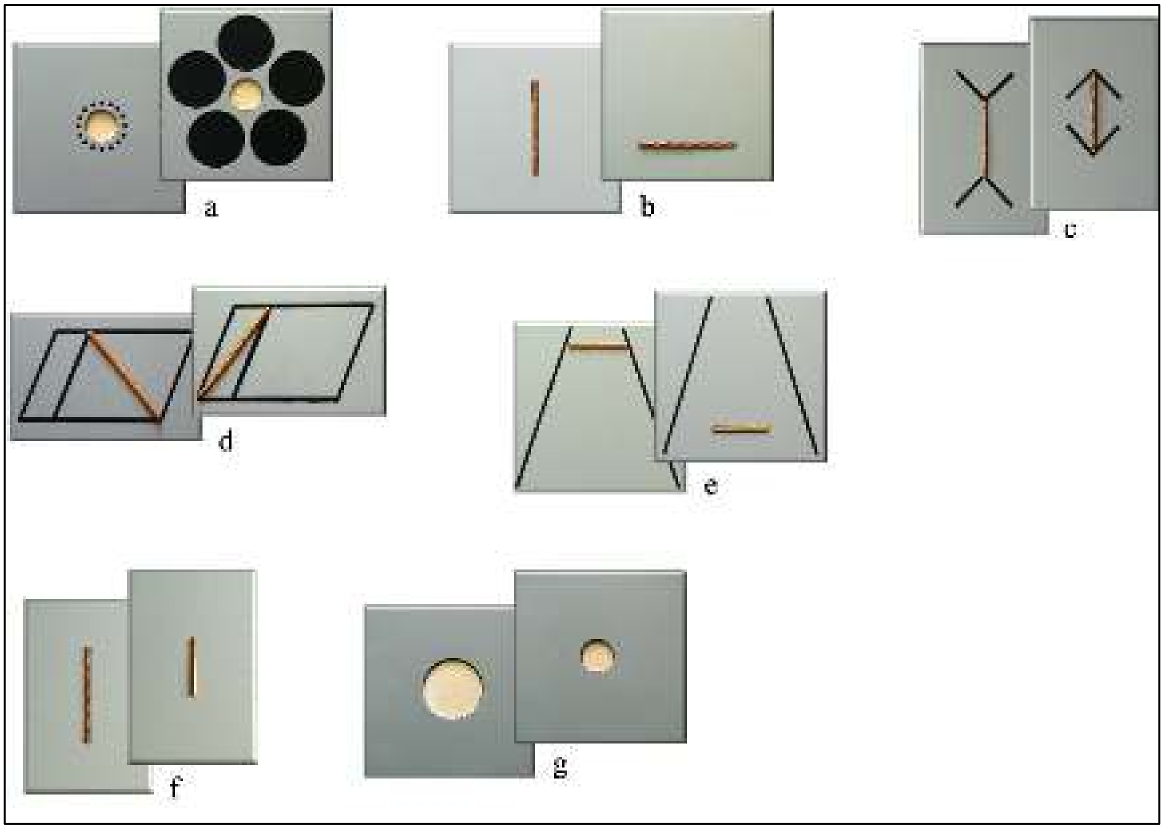

Figure 1

Test stimuli used: a) Ebbinghaus illusion, b) Horizontal-vertical illusion, c) Mueller-Lyer illusion, d) Sander illusion, e) Ponzo illusion, f) Stick control, g) Circle control. For each stimulus pair the left board is supposed to display the illusionary or actual bigger food item.

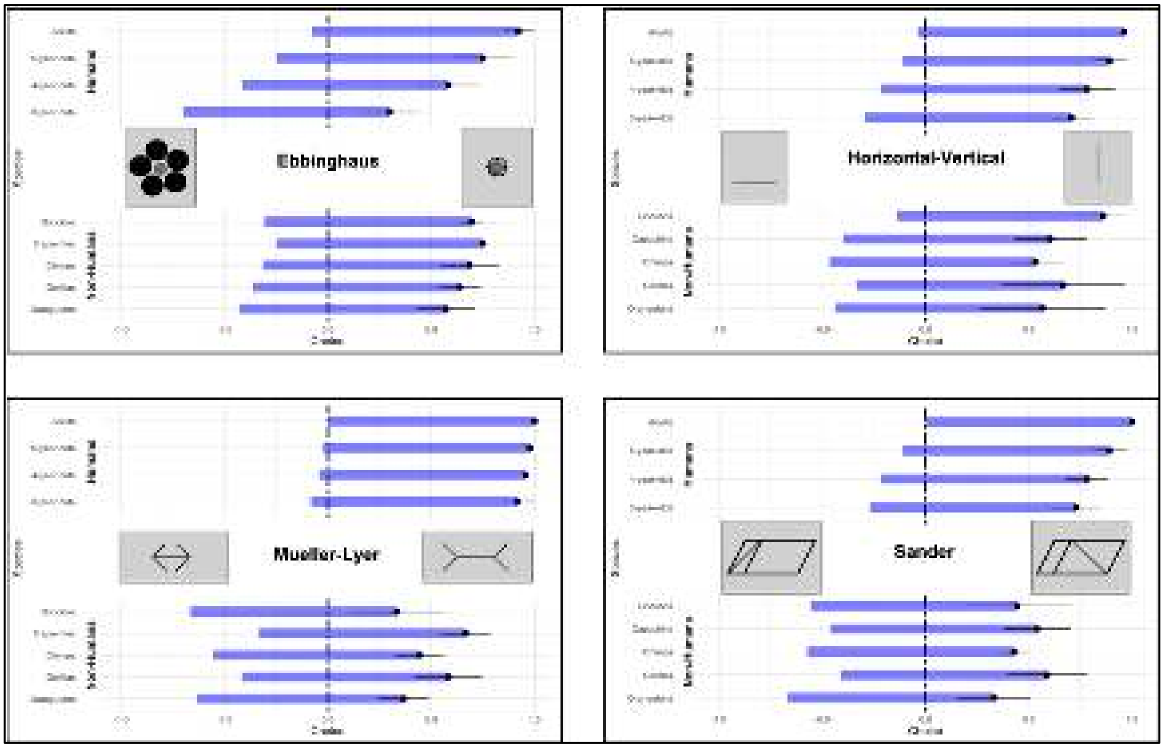

Figure 2

Group performance of the five nonhuman primate species (Bonobos, Chimpanzees, Gorillas, Orangutan, Capuchins) and the human subjects of different ages (3 years, 4 years, 5 years, adults). Beams represent mean proportion of trials in which subjects chose the illusionary smaller (left) or larger (right) stimulus for each of the four illusions. Whiskers indicate 95% CIs.

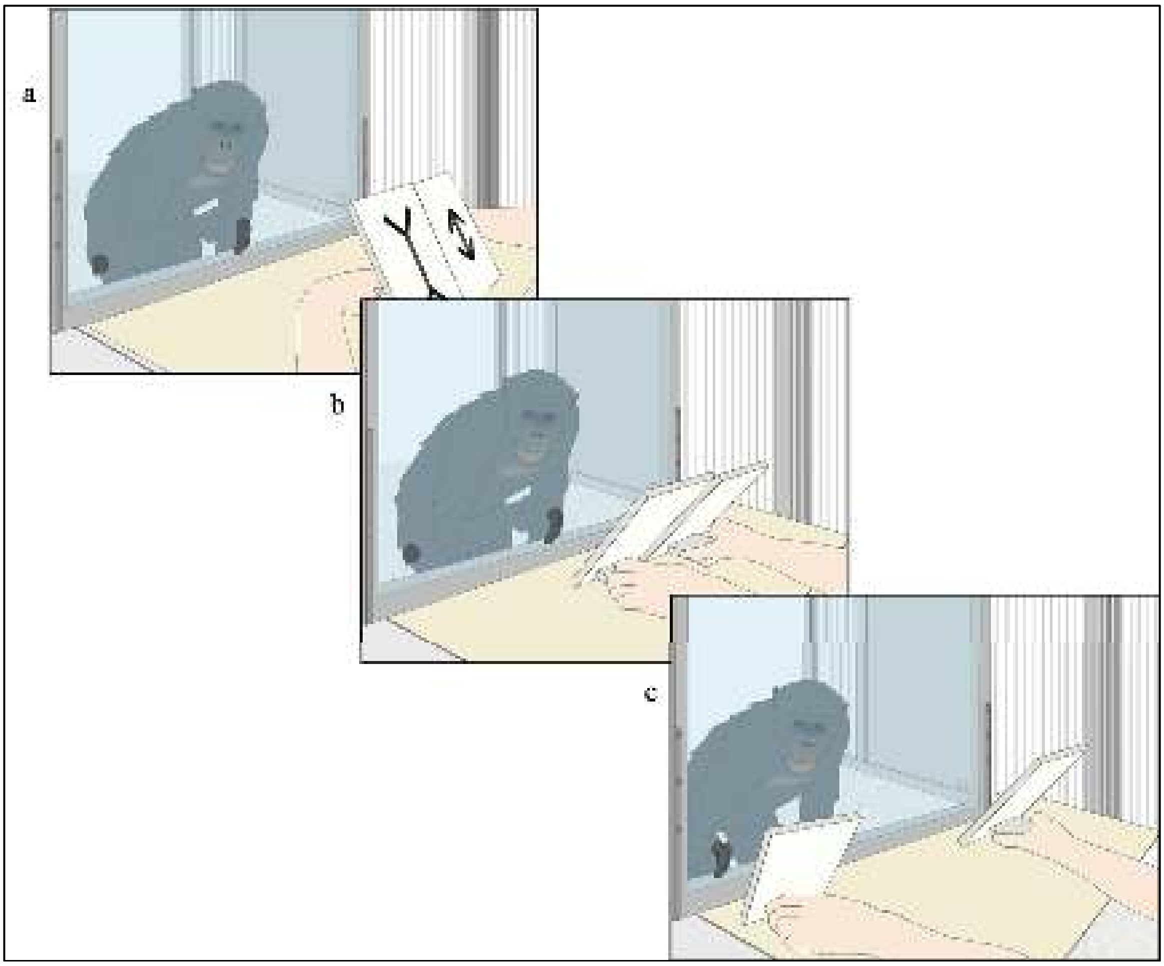

Figure 3

At the beginning of a trial the stimuli are turned away from the subject and baited with food (a). Next, the stimuli were turned towards the subject for 3-5 seconds (b) before they were moved forward in order to allow the subject to indicate its choice (c).