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ORIGINAL PAPER

From colour photographs to black-and-white line drawings: an assessment of chimpanzees' (*Pan troglodytes*') transfer behaviour

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Abstract Over two experiments, we investigated the ability of two adolescent and two adult chimpanzees to generalise a learnt, pictorial categorisation to increasingly degraded and abstract stimuli. In Experiment 2, we further assessed the ability of the adolescent chimpanzees to engage in open-ended categorisation of black-and-white line drawings. The current results confirmed and extended previous findings, showing that sub-adult chimpanzees outperform adult chimpanzees in the categorisation of pictorial stimuli, particularly when the stimuli are more degraded and abstract in nature. However, none of the four chimpanzees showed positive transfer of their category learning to a set of black-and-white line drawings, and neither of the adolescent chimpanzees evidenced reliable open-ended categorisation of the black-and-white line drawings. The latter findings suggest that both sub-adult and adult chimpanzees find it difficult to recognise black-and-white line drawings, and that open-ended categorisation of black-and-white line drawings is challenging for chimpanzees.

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Introduction

A common feature of studies that have investigated the categorisation abilities of nonhuman animals (and humans) is the use of photographic stimuli in their different forms (e.g. full colour versus black and white). While it is difficult to ascertain the manner in which nonhuman animals perceive such stimuli (see Fagot 2000; also, Fagot et al. 2000; Fagot and Parron 2010; Weisman and Spetch 2010), the use of photographic stimuli has at least provided a consistent methodology, which has afforded ready cross-species comparison. Other kinds of degraded pictorial stimuli have also been used over the decades to probe the representational capacity of nonhuman animals, though. Arguably, the most interesting and challenging of these stimuli has been the use of line drawings, as they represent the most degraded pictorial form of a given object, devoid of almost all information content that is reliably present in an animal's everyday environment. As such, it has been argued that there has been no requirement (selective pressure) for animals to be able to recognise line drawings (Sayim and Cavanagh 2011), raising the intriguing possibility that this skill is uniquely human. However, as Sayim and Cavanagh state, "The ease and immediacy of recognising scenes and objects in simple line drawings [by human beings] suggests that, for the [human] visual system, line drawings have deep similarities to other more detailed visual representations as well as to the real scenes they depict" (2011, p. 1). Moreover, these deep similarities seem to be present in humans from a young age, with

5-month-old infants already showing effective line drawing recognition (DeLoache et al. 1979). This suggests that a period of learning is not a prerequisite for human beings' ability in line drawing recognition (see also Hochberg and Brooks 1962; but, see DeLoache et al. 1998). Given the above, it is important to ask whether the visual system of other animals—in particular other primates—similarly perceives deep similarities between line drawings and the real scenes or objects they depict.

In an early study investigating object-picture equivalence in pigeons, Cabe (1976) found that while pigeons perceived black-and-white photographs and white-on-black silhouettes as equivalent to solid objects, this was not the case for line drawings. Interestingly, this failure by pigeons to recognise the equivalence between real objects and their line drawing counterparts sat in contrast to earlier findings in rhesus macaques by Zimmerman and Hochberg (1971; see also Truppa et al. 2009). This allowed Cabe (1976) to speculate a possible divide between primates and other animals in the ability to comprehend line drawing stimuli. More recently, however, a number of authors have argued that such a divide is unlikely and that pigeons' perception of line drawings may be similar to that of humans (e.g. Kirkpatrick-Steger and Wasserman 1996; Kirkpatrick-Steger et al. 1996, 1998; Van Hamme et al. 1992; Wasserman et al. 1993).

Building on Zimmerman and Hochberg's (1971) work, more recent evidence has shown that chimpanzees also appear able to recognise the equivalence between real objects and line drawings. For example, Itakura (1994; see also Hayes and Hayes 1953) showed that a single, 12-year-old female chimpanzee named Ai was able to recognise line drawings of different, known humans, chimpanzees and an orangutan. In a more extensive assessment of chimpanzees' ability to generalise a learnt categorisation involving colour photographs to various kinds of degraded pictorial stimuli—i.e. coloured sketches, colour clip art (cartoon-like pictures) and black-and-white line drawings—Tanaka (2007) reported mixed results. In general, though, Tanaka's results showed a negative developmental trend in chimpanzees' ability to generalise a learnt, pictorial categorisation to increasingly degraded stimuli. Indeed, most interesting of all his results are those regarding the line drawing stimuli: while two of the three juvenile chimpanzees showed positive transfer of their previous category learning to the line drawings, none of the adult chimpanzees did. Furthermore, only one adult subject, Ai—compared to all three juvenile chimpanzees—came to learn to categorise the line drawings at a level significantly above chance over the course of the transfer test. Tanaka concluded from this that his results "revealed a clear difference between the adult and juvenile chimpanzees in their performance with line drawing images" (2007, p. 177). With regard to his conclusion, one point that goes in Tanaka's favour is that Ai had had previous experience with black-and-white line drawings (see Itakura 1994). One assumes it was based primarily on this fact that Tanaka (2007) went on to propose a critical period for the acquisition of pictorial competence in chimpanzees.

Tanaka's (2007) proposal is an intriguing one. Indeed, given human beings' close evolutionary history with chimpanzees, the notion of a critical period existing for the development of high-level pictorial competence in chimpanzees may have implications for child development. However, given that the basis of Tanaka's proposal is a single, small-scale study—and more realistically, a single individual (Ai)—it is also a bold hypothesis. Indeed, a multitude of factors may have played a role in enabling the juvenile chimpanzees in Tanaka's study to outperform the adult chimpanzees. For example, a broad body of evidence has shown that primates' visual function (see Andersen et al. 2010) and the flexibility of an animal's cognition are at their best when young (e.g. Adams et al. 2000; Bartus et al. 1979; Mell et al. 2005; Schoenbaum et al. 2002). It is, perhaps, for these reasons, then, that the juvenile chimpanzees in Tanaka's study outperformed the adult chimpanzees. It is also noteworthy that the categorisation procedure employed by Tanaka (2007) is not the simplest one: chimpanzees were required to select three flower stimuli from an array of 12 stimuli. This contrasts with the simpler, more commonly employed categorisation procedure in which only two stimuli are ever presented on the screen at the same time. Moreover, the chimpanzees in Tanaka's study received relatively few black-and-white line drawing test trials (80 in total) in which to assess their ability to learn the black-and-white line drawing categorisation. Finally, to the best of our knowledge, it is still an open question as to whether a chimpanzee—or any other nonhuman animal—which failed to show positive transfer of a learnt categorisation from photographic stimuli to black-and-white line drawings, would show positive transfer of a learnt categorisation from one set of black-and-white line drawings to a second set of novel, black-and-white line drawings (i.e. open-ended categorisation involving black-and-white line drawings).

The aim of the present study, therefore, was to further assess the categorisation behaviour of sub-adult and adult chimpanzees when generalising a learnt, pictorial categorisation to increasingly degraded and abstract stimuli. Moreover, we used a simpler and longer test procedure than that used by Tanaka (2007) to more fully assess chimpanzees' category learning ability. In Experiment 1, we assessed adolescent and adult chimpanzees' ability to generalise a learnt categorisation to degraded colour and black-and-white stimuli. In Experiment 2, we assessed adolescent and adult chimpanzees' ability to generalise their category learning to black-and-white line drawings. Furthermore, we assessed whether chimpanzees were able to engage in open-ended categorisation of black-and-white line drawings.

Experiment 1

In Experiment 1, chimpanzees were initially taught a categorisation which involved colour photographs of trees and flowers.[1] Subsequently, their transfer of this learnt categorisation to novel colour photographs, and to both coloured and black-and-white, sketch-like stimuli, was assessed. Based on the findings of Tanaka (2007), we predicted that while all chimpanzees would show excellent transfer of their category learning to the novel colour photographs, the adult chimpanzees would show poorer transfer of their category learning to the sketch-like stimuli than the adolescent chimpanzees. In particular, we expected any difference in this regard to be most pronounced for the black-and-white, sketch-like stimuli. It must be noted, however, that given the fact that both the coloured and black-and-white, sketch-like stimuli contained shading information, excellent transfer of their category learning to these stimuli was possible amongst all chimpanzees (see Reid and Spetch 1998).

Methods

Subjects

Two adolescent (Alex: aged 9 years 4 months; Alexandra: aged 10 years 10 months) and two adult (Trudi: aged 17 years 2 months; Fifi: aged 17 years 2 months) chimpanzees (*Pan troglodytes*), housed at the Wolfgang Köhler Primate Research Center, Zoo Leipzig, participated in the study. All subjects had touch screen experience, having participated in tasks which involved both 2-item discrimination and matching-to-samples. Furthermore, all participants had participated in a wide variety of non-touch-screen-based physical and social cognition tasks. In their early life, the two adolescent chimpanzees, Alex and Alexandra, were raised in a semi-enculturated environment by a human caregiver. Approximately 1 year prior to the present experiment, both Alex and Alexandra took part in an experiment which required them to engage in 2-item discriminations involving nine different black-and-white sketches of a human experimenter in various poses. Moreover, the aforementioned stimuli were already familiar to Alex, having previously been trained on a 'Do as I do' procedure using the black-and-white sketches. While it is difficult to know exactly how this previous experience with a limited set of black-and-white sketches affected their performance in the present study, it must been borne in mind by the reader. All chimpanzees were tested individually in a familiar, indoor observation room.

Apparatus and stimuli

A 21-inch Hansol 2100A CRT touch screen monitor (Model No.: 103FH) connected to a PC computer—outputting a display resolution of 1,600 × 1,200 pixels at a refresh rate of 60 Hz, and running E-Prime 1.2 software (Psychology Software Tools, Inc., Schneider et al. 2002)—was used. The monitor sat on a small table which was positioned directly in front of one Plexiglas panel which separated the chimpanzee subject from the experimenter. Five circular finger holes (one positioned in the centre of the Plexiglas panel and four that surrounded this central hole located towards the top-left, bottom-left, top-right and bottom-right corners) measuring 6 cm in diameter were cut into the Plexiglas panel to enable safe touching of the touch screen monitor by the chimpanzees. Two Logitech speakers (Model No.: S-120), which were positioned on the floor on either side of the small table and which faced towards the chimpanzees, were used to present audio feedback. Small pieces of crushed-up banana pellet were used as a reward and were fed by hand through an opaque, black plastic tube which was located next to the small table. A low white plastic stool was used by the experimenter to sit on during testing.

Our base stimuli were 15 colour photographs of trees and 15 colour photographs of flowers, which were freely sourced from the Internet. Each base stimulus comprised either a single colour image of a tree or a single colour image of a flower. All images were scaled to approximately the same size and were presented in the centre of a 350 × 350 pixel white square. Using Adobe Photoshop's 'Colored Pencils' and 'Graphic Pen' tools, we further created both coloured and black-and-white, sketch-like stimuli of ten of the base stimuli in each category, respectively (see Fig. 1 for examples). These computer-generated, sketch-like stimuli included shading information which was derived from the base stimuli. In total, a pool of 70 stimuli was created: 35 tree stimuli (15 colour photographs, 10 coloured, sketch-like stimuli and 10 black-and-white, sketch-like stimuli) and 35 flower stimuli (15 colour photographs, 10 coloured, sketch-like stimuli and 10 black-and-white, sketch-like stimuli).

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[1] As noted by one anonymous reviewer, it is uncertain as to whether the chimpanzees came to process and consider only one class of stimulus—neglecting the other—or both classes of stimuli. Whatever the case, this issue has no bearing on the findings from the test phases of Experiments 1 and 2.

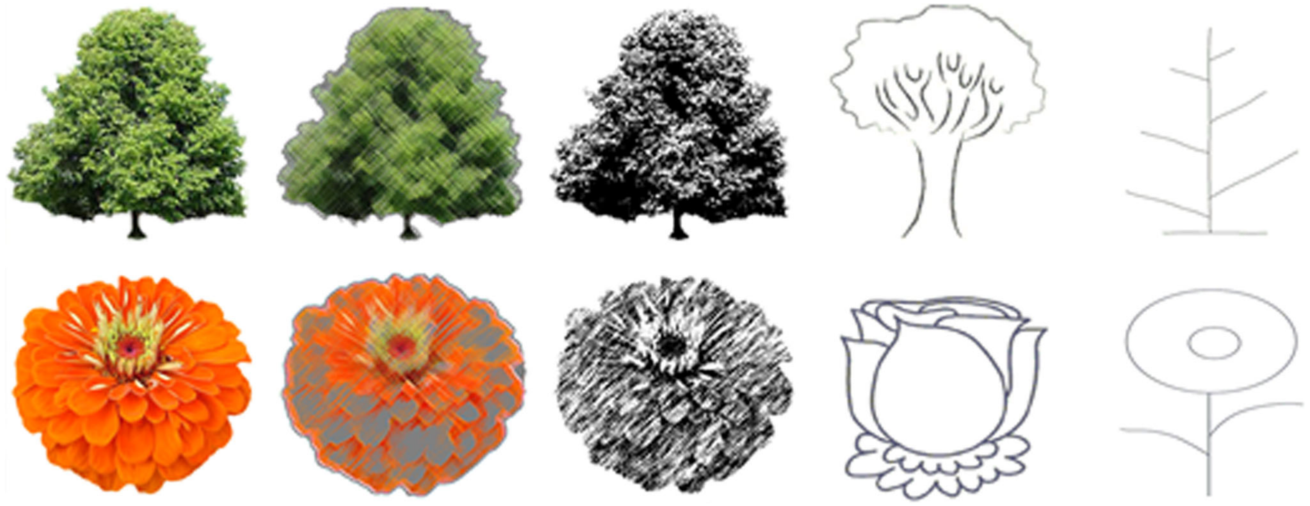

Fig. 1 Examples of the tree and flower stimuli used in Experiments 1 and 2 in their different forms: *colour photographs*; *coloured*, *sketch-like stimuli*; *black-and-white*, *sketch-like stimuli*; *black-and-white line drawings*. The final tree and flower stimuli are examples of probably the most degraded and abstract *black-and-white line drawings* presented in each category. The tree stimuli occupy the *upper line* while the flower stimuli occupy the *lower line*

Design and procedure

Due to the small sample size, a within-subjects design—focused at the individual level—was employed. Although no formal (statistical) between-subjects analysis was undertaken, where pertinent, descriptive comparisons between the two groups of chimpanzees (Sub-Adult and Adult) were made.

Experiment 1 consisted of an initial acquisition phase followed by a test phase. For each category of stimulus (Tree and Flower), ten of the base (colour photograph) stimuli were randomly selected and presented during the acquisition phase. From these, five stimuli from each stimulus category were randomly selected to act as *control stimuli*, being further presented during the test phase. Primary interest, however, concerned the chimpanzees' performance with the novel stimuli presented during the test phase. These stimuli formed five transfer conditions: New_Photo (the base (colour photograph) stimuli not presented during the acquisition phase); Old_CS (the computer-generated, coloured, sketch-like versions of the control stimuli); New_CS (the computer-generated, coloured, sketch-like versions of the base stimuli not presented during the acquisition phase); Old_BWS (the computer-generated, black-and-white, sketch-like versions of the control stimuli) and New_BWS (the computer-generated, black-and-white, sketch-like versions of the base stimuli not presented during the acquisition phase). For all chimpanzees, touches to the tree stimuli were rewarded with food and touches to the flower stimuli were nonrewarded.

In both the acquisition phase and the test phase, the background colour of the screen was black and each trial consisted of the following procedure: initially, a white fixation point (measuring 150 × 150 pixels) was presented in the centre of the screen. Surrounding the white fixation point, we defined an area of touch of 350 × 350 pixels; a touch anywhere within this area resulted in the immediate presentation of one tree stimulus and one flower stimulus. Any touch made outside the area of touch had no consequence. Selection of the tree and flower stimuli was random without replacement. As such, following presentation of a given stimulus, it was not available for selection again until the remaining stimuli had been presented. This fact meant that a stimulus could only be presented a maximum of twice in succession. The positioning of the tree and flower stimuli on the screen on each trial was chosen randomly from 12 pre-defined configurations.[2] A touch anywhere within the 350 × 350 pixel area of a tree stimulus resulted in the immediate termination of the stimuli, presentation of a positive sounding sound and a food reward being given. Following a 750-ms black screen inter-trial interval (ITI), a new trial began with presentation of the white fixation point. A touch anywhere within the 350 × 350 pixel area of a flower stimulus resulted in the immediate termination of the stimuli, presentation of a negative sounding sound and no food reward being given. Following a 5,000-ms green screen 'punishment phase' (ITI), a new trial began with presentation of the white fixation point.

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[2] (1) Stim. 1 top-left–Stim. 2 top-right; (2) Stim. 1 top-right–Stim. 2 top-left; (3) Stim. 1 bottom-left–Stim. 2 bottom-right; (4) Stim. 1 bottom-right–Stim. 2 bottom-left; (5) Stim. 1 top-left–Stim. 2 bottom-left; (6) Stim. 1 bottom-left–Stim. 2 top-left; (7) Stim. 1 top-right–Stim. 2 bottom-right; (8) Stim. 1 bottom-right–Stim. 2 top-right; (9) Stim. 1 top-left–Stim. 2 bottom-right; (10) Stim. 1 bottom-right–Stim. 2 top-left; (11) Stim. 1 top-right–Stim. 2 bottom-left; (12) Stim. 1 bottom-left–Stim. 2 top-right (Stim. 1 = tree stimulus & Stim. 2 = flower stimulus).

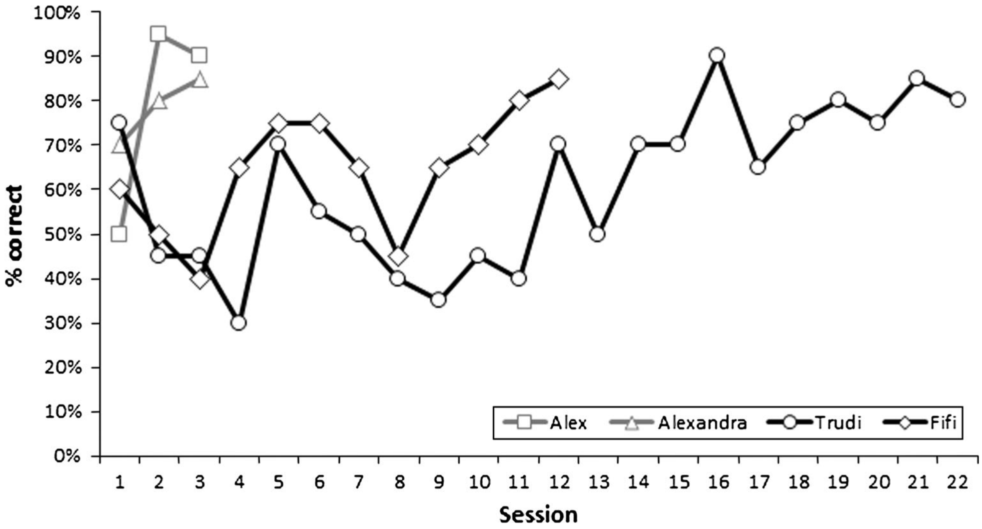

Fig. 2 Percentage of correct responses in each session during acquisition of the initial (*colour photograph*) categorisation in Experiment 1

During the test phase, it was only ever the case that tree and flower stimuli drawn from the same condition were presented on the screen together. As such, while a trial could consist of one tree stimulus and one flower stimulus both drawn from condition New_Photo being presented together, a trial could not consist of one tree stimulus drawn from condition New_Photo and one flower stimulus drawn from condition Old_CS being presented together, for example. The presentation order of the different conditions was pseudorandom, with the constraint that stimuli from the same condition could not be presented more than twice in succession. To maintain a high level of motivation amongst the chimpanzees throughout the experiment, differential reinforcement was used in both the acquisition and test phases.

Each session of the acquisition phase consisted of 20 trials, meaning that each stimulus was presented twice over the course of a session. The acquisition phase continued until a subject had achieved a response accuracy of at least 80 % correct (16 out of 20 correct; $p = .01$, Binomial Test) over two consecutive sessions, whereby they were transferred to the test phase. The test phase took place over ten sessions, with one session involving five trials of each of the different transfer conditions and five trials of the control stimuli. Over the course of a test session, therefore, the 30 tree and 30 flower stimuli were each presented once.

Performance was assessed at an individual level using nonparametric two-tailed, exact tests.

Results and discussion

Acquisition

The acquisition rates for the initial categorisation involving the base stimuli for the four chimpanzees are shown in Fig. 2. As can be seen, while all the chimpanzees successfully acquired the categorisation, the two adolescent chimpanzees, Alex and Alexandra, did so at a much faster rate.

Test

Focussing on the data from the test phase, interest concerned the performance of the chimpanzees over the first four sessions (20 trials) of conditions New_Photo, Old_CS, New_CS, Old_BWS and New_BWS. Such analysis enables a direct comparison to be made with the chimpanzees' performance during the acquisition phase and, we believe, represents a fair assessment of any immediate positive transfer of their category learning to the transfer conditions, rather than any new learning—which was a concern given the continued use of differential reinforcement at Test. Where appropriate, we further compared a chimpanzee's performance over the first and last four sessions (20 trials) of the test phase to assess whether any learning had taken place.

Adolescent chimpanzees

Over the ten sessions of the test phase, both Alex and Alexandra maintained excellent performance with the control stimuli (Ms = 100 and 84 % correct, respectively).

Figure 3 shows Alex's and Alexandra's performance over the first four and last four sessions of the test phase, split by the five transfer conditions. As can be seen, Alex performed extremely well, exhibiting response accuracies at or above 80 % correct in all transfer conditions over the first four sessions. A 2 × 5 Fisher's exact test revealed no significant association between Alex's response accuracy and transfer condition over the first four sessions ($p = .54$). Binomial tests confirmed that Alex's performance over the

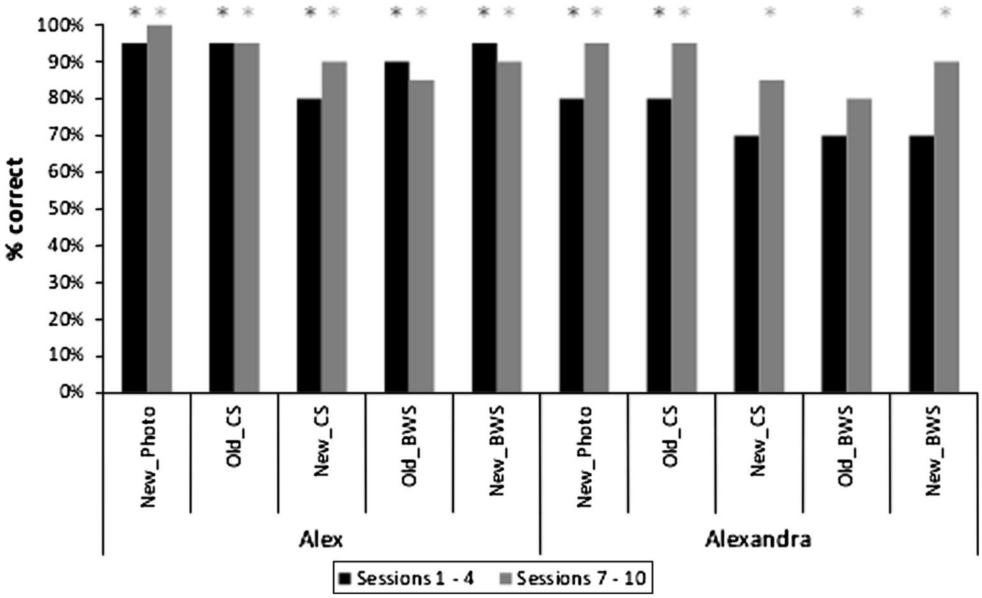

Fig. 3 Percentage of correct responses for the adolescent chimpanzees over the first four and last four sessions of the test phase of Experiment 1, split by transfer condition. *Asterisks* denote significantly above-chance performance

first four sessions of all the transfer conditions was significantly above chance (smallest $p = .01$).

Alexandra also performed well, although generally a little worse than Alex over the first four sessions of the test phase—particularly in conditions New_CS, Old_BWS and New_BWS. A 2 × 5 Fisher's exact test revealed no significant association between Alexandra's response accuracy and transfer condition over the first four sessions ($p = .87$). However, binomial tests revealed that while Alexandra's performance over the first four sessions of conditions New_Photo and Old_CS was significantly above chance (both ps = .01), her performance over the first four sessions of conditions New_CS, Old_BWS and New_BWS was not significantly above chance (all ps = .12). A 2 × 2 Fisher's exact test revealed that, overall, Alexandra performed significantly better over the last four sessions than over the first four sessions ($p = .01$), suggesting that some learning took place over the course of the test phase. Indeed, binomial tests revealed that Alexandra's performance over the last four sessions of all the transfer conditions was significantly above chance (smallest $p = .01$).

Adult chimpanzees

Like Alex and Alexandra, over the ten sessions of the test phase, Fifi maintained excellent performance with the control stimuli ($M = 92$ % correct). Trudi's performance with the control stimuli, on the other hand, dropped substantially at Test and was rather poor ($M = 60$ % correct). One can only assume that this drop in performance resulted from a degree of confusion caused by the introduction of the novel stimuli. Notably, however, Trudi's response accuracy with the control stimuli was at 75 % correct over the last four sessions of the test phase. Whatever the cause of Trudi's poor performance with the control stimuli at Test, given such, her performance in the transfer conditions needs to be treated with caution.

Figure 4 shows Trudi's and Fifi's performance over the first four and last four sessions of the test phase, split by the five transfer conditions. It is clear that Trudi's performance was generally poor and rather variable across the transfer conditions. A 2 × 5 Fisher's exact test revealed no significant association between Trudi's response accuracy and transfer condition over the first four sessions ($p = .69$). Binomial tests revealed that her performance over the first four sessions only significantly exceeded chance in condition New_BWS ($p = .04$; all other ps $> .05$). While Trudi appeared to evidence some learning in the three transfer conditions which involved the colour stimuli over the course of the test phase, a 2 × 2 Fisher's exact test revealed that, overall, her performance over the last four sessions of the test phase was not significantly different from her performance over the first four sessions ($p = .29$). However, binomial tests revealed that, over the last four sessions, Trudi's performance was significantly above chance in conditions New_Photo, Old_CS and New_CS (smallest $p = .04$), but not in conditions Old_BWS and New_BWS (largest $p = .26$).

In contrast to Trudi, Fifi's performance over the first four sessions of the test phase was good in all transfer conditions except condition New_BWS, where she achieved a response accuracy of only 55 % correct. Although a 2 × 5 Fisher's exact test revealed no significant association between Fifi's response accuracy and transfer condition over the first four sessions ($p = .37$), binomial tests confirmed that, over this same period, her

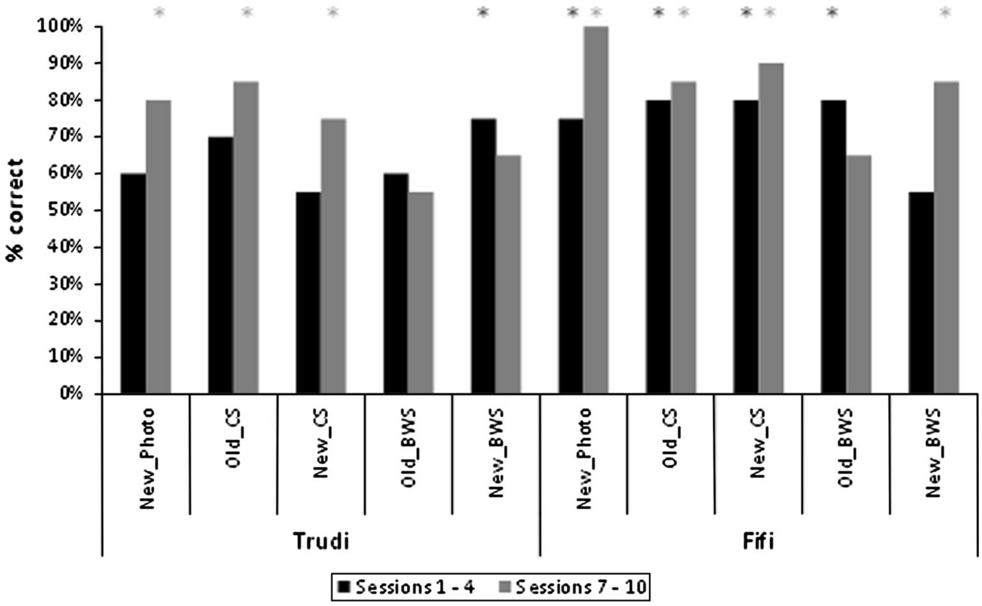

Fig. 4 Percentage of correct responses for the adult chimpanzees over the first four and last four sessions of the test phase of Experiment 1, split by transfer condition. *Asterisks* denote significantly above-chance performance

performance was significantly above chance in all transfer conditions (smallest $p = .04$) except condition New_BWS ($p = .82$). Strangely, while Fifi's performance in condition New_BWS improved (numerically) over the course of the test phase, this improvement was somewhat at the expense of her performance in condition Old_BWS, which worsened (numerically) over the same period; indeed, binomial tests revealed that, over the last four sessions, Fifi's performance was significantly above chance in all transfer conditions (smallest $p = .003$) except condition Old_BWS ($p = .26$). A 2 × 2 Fisher's exact test revealed that, overall, Fifi's performance over the last four sessions was not significantly different from her performance over the first four sessions ($p = .08$).

Taken as a whole, it is apparent that the adult chimpanzees experienced the greatest difficulty categorising the black-and-white, sketch-like stimuli at Test. Moreover, the adult chimpanzees experienced greater difficulty than the adolescent chimpanzees categorising all of the black-and-white, sketch-like stimuli over the course of the test phase. As stated above, however, although we cannot be certain how the adolescent chimpanzees' previous experience with a limited set of black-and-white sketches influenced the present results, it is possible it facilitated their performance.

Experiment 2

In Experiment 2, we built on the above results by presenting the chimpanzees with black-and-white line drawings, of trees and flowers; for, it was with stimuli like these that the clearest difference in performance between Tanaka's juvenile and adult chimpanzees were found. We also sought to extend the work of Tanaka (2007) by assessing whether those chimpanzees which failed to show positive transfer of their category learning from Experiment 1 to a set of black-and-white line drawings, were, however, able to form open-ended categories of the latter stimuli.

Methods

Subjects

The subjects from Experiment 1 participated in Experiment 2.

Apparatus and stimuli

The same apparatus used in Experiment 1 was used in Experiment 2. Stimuli were the control stimuli of Experiment 1, and black-and-white line drawings of ten trees and ten flowers, which were freely sourced from the Internet (see Fig. 1 for examples). The black-and-white line drawings were divided randomly and equally into two sets of stimuli (Set 1 and Set 2), with both sets containing five tree stimuli and five flower stimuli. As for the control stimuli, each black-and-white line drawing comprised either a single tree image or a single flower image. All images were scaled to approximately the same size and were presented in the centre of a 350 × 350 pixel white square.

As some of the black-and-white line drawings were somewhat abstract in nature, we felt it prudent to assess in human participants a) whether the tree stimuli were readily identifiable as trees, and b) whether the tree stimuli were equally identifiable in the two stimulus sets. We found that the human participants were able to identify the black-and-white line drawings of trees with near perfect accuracy. Moreover, the black-and-white line drawings of trees were equally identifiable in both stimulus sets (Set 1 and Set 2). Given the similarities that exist between human and chimpanzee visual perception (see, e.g. Grether 1940a, b, c; Jacobs et al. 1996; Matsuno and Tomonaga 2008; Matsuzawa 1990; Tomonaga 2001; Tomonaga and Matsuzawa 1992), these findings indicated that the two classes of stimuli should be equally discriminable and, as such, equally easy for the chimpanzees to categorise within both stimulus sets (see Supplementary Material for further details).

Design and procedure

The same analytical approach detailed in Experiment 1 was used. Experiment 2 primarily consisted of two phases: Test 1 and Test 2. Along with the control stimuli, which were presented in both phases, the black-and-white line drawings of Set 1 were presented in Test 1 (henceforth, termed condition New_BWL1), and the black-and-white line drawings of Set 2 were presented in Test 2 (henceforth, termed condition New_BWL2) for all chimpanzees. As in Experiment 1, a touch to the tree stimuli was rewarded with food and a touch to the flower stimuli was nonrewarded for all chimpanzees. A similar trial procedure to that of the acquisition phase of Experiment 1 was employed in the two test phases, with the following differences: Test 1 continued until a subject had achieved a response accuracy in condition New_BWL1 of at least 80 % correct (16 out of 20 correct; $p = .01$, Binomial Test) over two consecutive blocks, where one block comprised two sessions. On attainment of this criterion, the chimpanzees were transferred to Test 2, which proceeded for a total of six blocks (12 sessions). If a chimpanzee failed to reach the transfer criterion of Test 1 after 20 blocks (40 sessions), the experiment was ended for that chimpanzee and Test 2 was not completed.

Results and discussion

Test 1

Adolescent chimpanzees

Over the course of Test 1, Alex and Alexandra continued to maintain their excellent performance with the control stimuli (*M*s = 98 and 97 % correct, respectively). Figure 5 shows Alex's and Alexandra's performance in condition New_BWL1 across Test 1, split by block. As can be seen, their performance in condition New_BWL1 was initially very poor, evidencing no sign of any positive transfer of their previous category learning to the black-and-white line drawings. Considering his performance in the test phase of Experiment 1, this finding is particularly surprising for Alex. Comparing Alex's and Alexandra's performance over the first block of condition New_BWL1 to their performance over the same period in condition New_BWS—arguably the most comparable set of stimuli from Experiment 1—Alex exhibited a 35 % drop in performance in condition New_BWL1 and Alexandra exhibited a 20 % drop in performance in condition New_BWL1. Focussing on their performance over Block 1 (first 20 trials) of

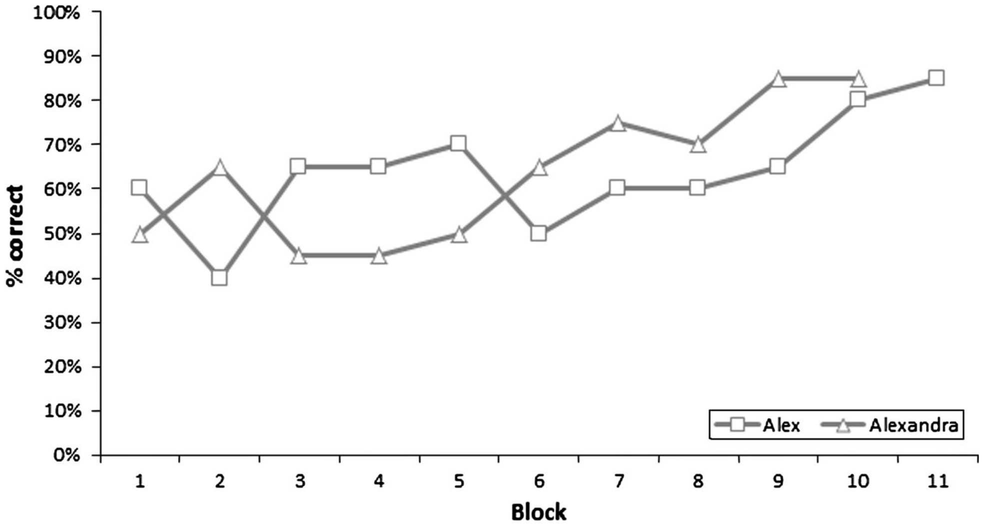

Fig. 5 Percentage of correct responses for the adolescent chimpanzees to the *black-and-white line drawings* presented in Test 1 (condition New_BWL1) of Experiment 2, split by block—where one block represents two sessions

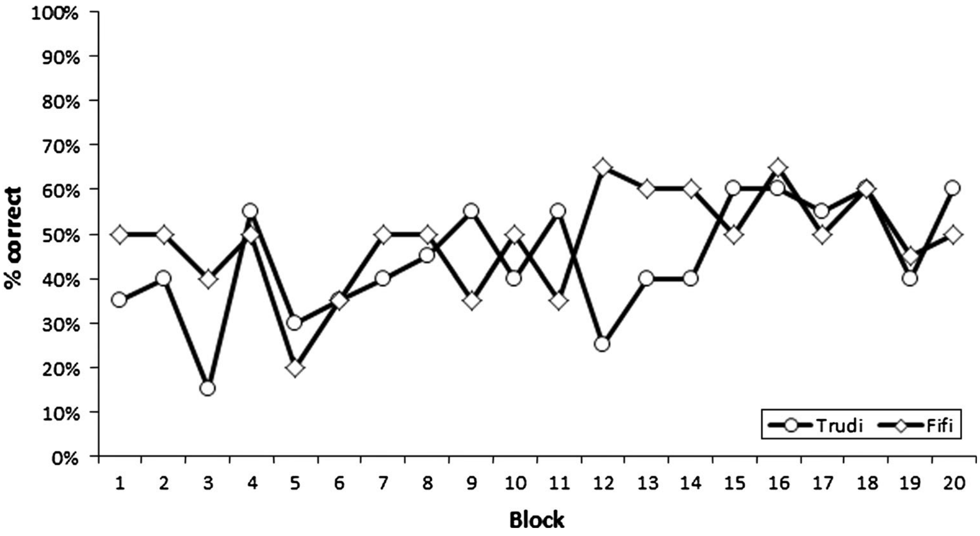

Fig. 6 Percentage of correct responses for the adult chimpanzees to the *black-and-white line drawings* presented in Test 1 (condition New_BWL1) of Experiment 2, split by block—where one block represents two sessions

condition New_BWL1, binomial tests confirmed that neither Alex's nor Alexandra's response accuracy was significantly above chance (largest $p = .50$). However, both Alex and Alexandra acquired the black-and-white line drawing categorisation of condition New_BWL1 after a moderate period of training (Alex: 220 trials; Alexandra: 200 trials).

Adult chimpanzees

Over the course of Test 1, Trudi showed good performance with the control stimuli ($M = 79$ % correct) and Fifi continued to maintain her excellent performance with these stimuli ($M = 97$ % correct). Figure 6 shows Trudi's and Fifi's performance in condition New_BWL1 across Test 1, split by block. As for the adolescent chimpanzees, the adult chimpanzees evidenced no sign of any positive transfer of their previous category learning to the black-and-white line drawings. Comparing Trudi's and Fifi's performance over the first block of condition New_BWL1 to their performance over the same period in condition New_BWS, Trudi exhibited a 40 % drop in performance in condition New_BWL1 and Fifi exhibited a 5 % drop in performance in condition New_BWL1. Like the adolescent chimpanzees, then, the adult chimpanzees' performance over Block 1 (first 20 trials) of condition New_BWL1 was very poor. Binomial tests confirmed that neither Trudi's ($p = .26$ (below chance performance)) nor Fifi's ($p = 1.00$) response accuracy was significantly above chance. What is notable about the adult chimpanzees' performance in condition New_BWL1, though—and in direct contrast to the adolescent chimpanzees—is that neither of them exhibited any sign of learning the black-and-white line drawing categorisation over the entire 20 blocks of Test 1. This staggering failure—especially on the part of Fifi—is highlighted by the fact that even after 20 blocks (400 trials) of condition New_BWL1, both Trudi's and Fifi's response accuracy was still rooted at the chance level (Trudi: 60 % correct, $p = .50$; Fifi: 50 % correct, $p = 1.00$, Binomial tests).

As for the results of Experiment 1, it is important to highlight that although we cannot be certain how the adolescent chimpanzees' previous experience with a limited set of black-and-white sketches influenced the present results, it is possible it facilitated their performance. Given the adult chimpanzees' failure to learn the categorisation of condition New_BWL1 within the pre-defined limit, only the adolescent chimpanzees were transferred to Test 2 to assess the open-ended nature of their category learning in condition New_BWL1.

Test 2

Alex continued to maintain his excellent performance with the control stimuli ($M = 100$ % correct). Figure 7 shows Alex's performance in condition New_BWL2, split by block—for comparison, his performance across the first six blocks of condition New_BWL1 is included. As in Test 1, Alex evidenced little sign of clear positive transfer of his previous category learning to the novel, black-and-white line drawings of condition New_BWL2. Indeed, his Block 1 performance in condition New_BWL2 was identical to his Block 1 performance in condition New_BWL1. Notably, however, Alex attained an 80 % response accuracy much faster in condition New_BWL2 (Block 2) than in condition New_BWL1 (Block 10). All things considered, this was quite an improvement in performance.

Focussing on his performance in Block 1 (first 20 trials) of condition New_BWL2, a binomial test revealed that Alex's response accuracy was not significantly above

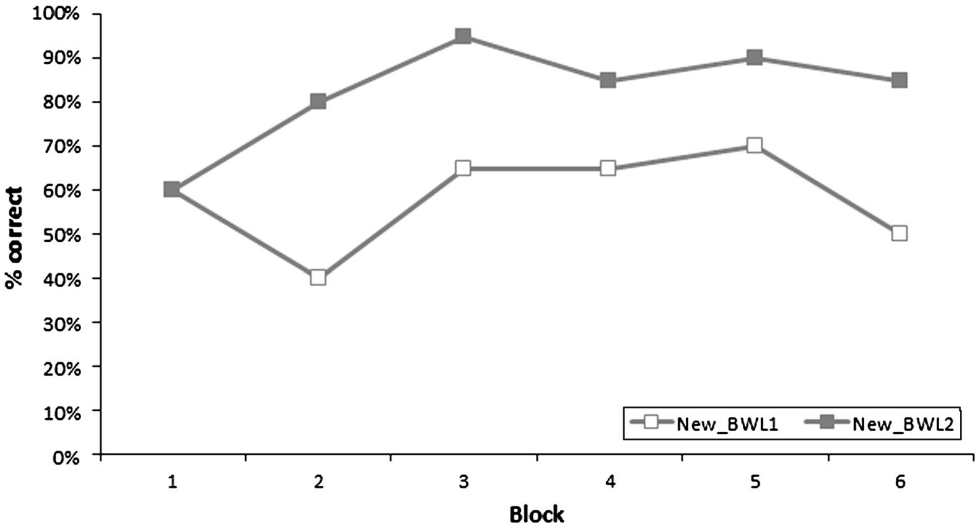

Fig. 7 Percentage of Alex's correct responses to the *black-and-white line drawings* presented in Test 2 (condition New_BWL2) of Experiment 2, split by block—where one block represents two sessions. For comparison, Alex's performance over the equivalent period in condition New_BWL1 is included

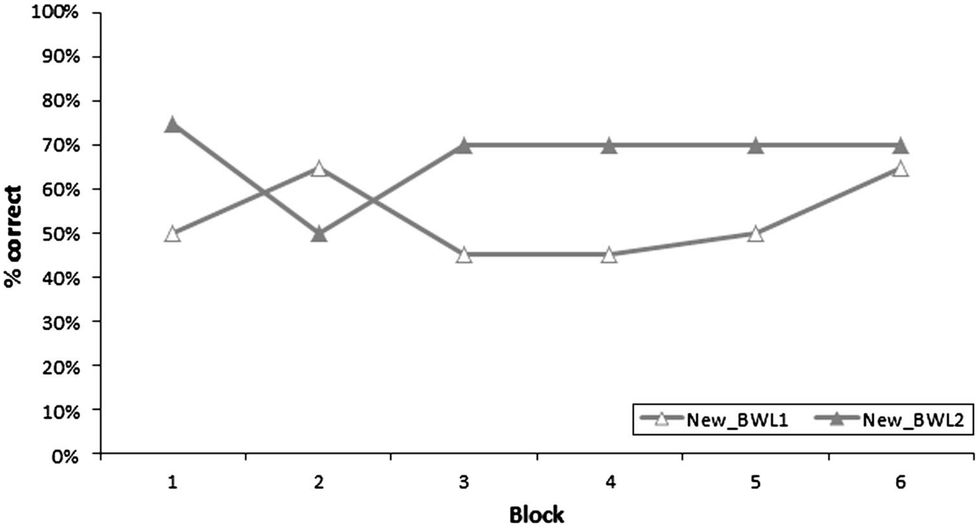

Fig. 8 Percentage of Alexandra's correct responses to the *black-and-white line drawings* presented in Test 2 (condition New_BWL2) of Experiment 2, split by block—where one block represents two sessions. For comparison, Alexandra's performance over the equivalent period in condition New_BWL1 is included

chance ($p = .50$). However, comparing his overall performance in condition New_BWL2 to his performance over the same period in condition New_BWL1, a Mann–Whitney U test revealed that Alex performed significantly better in condition New_BWL2 than in condition New_BWL1 ($U(6, 6) = .00$, $p = .002$).

Alexandra also continued to maintain her excellent performance with the control stimuli ($M = 98$ % correct). Figure 8 shows Alexandra's performance in condition New_BWL2, split by block—for comparison, her performance across the first six blocks of condition New_BWL1 is included. Unlike Alex, Alexandra appeared to show some positive transfer of her previous category learning to the novel, black-and-white line drawings of condition New_BWL2, achieving a response accuracy of 75 % correct in Block 1 (first 20 trials). However, this high level of performance in Block 1 has to be weighed against the fact that her response accuracy subsequently dropped dramatically to only 50 % correct in Block 2, before remaining stable at 70 % correct in Blocks 3–6. Notably, though, like Alex, Alexandra's overall performance in condition New_BWL2 was somewhat better than her performance over the equivalent period in condition New_BWL1.

Focussing on her performance in Block 1 (first 20 trials) of condition New_BWL2, a binomial test revealed that Alexandra's response accuracy was significantly above chance ($p = .04$). Comparing her overall performance in condition New_BWL2 to her performance over the same period in condition New_BWL1, a Mann–Whitney U test revealed that Alexandra performed significantly better in condition New_BWL2 than in condition New_BWL1 ($U(6, 6) = 3.00$, $p = .01$).

Based on the results from the human participants (see Supplementary Material), two possible mechanisms exist to account for the adolescent chimpanzees' better performance in condition New_BWL2 than in condition New_BWL1: Firstly, the adolescent chimpanzees formed open-ended categories of the black-and-white line drawings presented in condition New_BWL1. Secondly, during their experience with the black-and-white line drawings of condition New_BWL1, there was a degree of perceptual learning towards the stimuli, which subsequently increased the level of discriminability of the black-and-white line drawings of condition New_BWL2 (see, e.g. Goldstone 1998; Hall 1991). Critically, the second mechanism suggests that the adolescent chimpanzees did nothing more than rote learn the categorisation of condition New_BWL1. This idea gains credence from the fact that Alex—who, for the most part, has been the best performing chimpanzee—showed a poor level of performance in Block 1 of condition New_BWL2, and from the fact that Alexandra failed to maintain a consistent response accuracy of at least 75 % correct in Blocks 2–5 of condition New_BWL2. Taken as a whole, therefore, we believe that the results of Test 2 indicate that the adolescent chimpanzees most likely failed to form open-ended categories of the black-and-white line drawings presented in condition New_BWL1.

General discussion

Using a simple categorisation procedure, the present paper sought to further assess the categorisation behaviour of sub-adult and adult chimpanzees when generalising a learnt, pictorial categorisation to coloured and black-and-white, sketch-like stimuli (Experiment 1), and to black-and-white line drawings (Experiment 2).

In Experiment 1, we found that the adolescent chimpanzees generally outperformed the adult chimpanzees. Moreover, this difference in performance between the adolescent and adult chimpanzees was particularly evident for the black-and-white, sketch-like stimuli—i.e. the most degraded stimuli used in Experiment 1. Overall, these results are broadly consistent with the findings of Tanaka (2007). It must be highlighted, however, that, unlike Alex, Alexandra did not show reliable positive transfer of her category learning to all of the transfer conditions of Experiment 1. Based on Tanaka's (2007) critical period hypothesis, this was not what was predicted. Taken as a whole, therefore, we suggest that the results of Experiment 1 provide only partial support for Tanaka (2007).[3]

In Experiment 2, we found that none of the chimpanzees showed positive transfer of their category learning to the first set of black-and-white line drawings. However, whereas the adolescent chimpanzees learnt to categorise the black-and-white line drawings of Test 1 after a moderate period of training, neither of the adult chimpanzees displayed any such learning, even after the maximum 400 test trials. As for Experiment 1, the better performance of the adolescent chimpanzees in Test 1 of Experiment 2 is broadly consistent with the findings of Tanaka (2007). However, the poor performance of the adolescent chimpanzees in the early blocks of Test 1 is troubling—especially where Alex is concerned. In keeping with the conclusions from Experiment 1, we suggest that the results from Test 1 of Experiment 2 similarly provide only partial support for Tanaka (2007).

The most surprising result of Experiment 2 is that the adolescent chimpanzees did not reliably transfer their category learning from the black-and-white line drawings of Test 1 to the black-and-white line drawings of Test 2. It is, however, interesting that their overall performance with the black-and-white line drawings of Test 2 was significantly better than their performance with the black-and-white line drawings of Test 1. While it is difficult to be sure of the exact mechanism that afforded this better performance in Test 2, as discussed previously, we believe it was most likely the result of perceptual learning following experience with the black-and-white line drawings of Test 1. The above is important because it suggests that the adolescent chimpanzees did not form open-ended categories of the black-and-white line drawings of Test 1. Indeed, for all the chimpanzees, it is clear that they performed much better in the transfer conditions of Experiment 1 (New_Photo, Old_CS, New_CS, Old_BWS and New_BWS) than over the equivalent period in the transfer condition(s) of Experiment 2 (New_BWL1 and, for the adolescent chimpanzees, New_BWL2).

The difficulty experienced by the chimpanzees in categorising the black-and-white line drawings of Experiment 2 contrasts sharply with the ease with which the human participants were able to do this. This difference in performance indicates that, for the chimpanzee visual system, black-and-white line drawings do not always share a high degree of similarity with more detailed visual representations (cf. Itakura 1994; Tanaka 2007). Overall, then, the findings of Experiment 2 suggest that chimpanzees find it difficult to recognise black-and-white line drawings, and that open-ended categorisation of black-and-white line drawings is challenging for chimpanzees.

A number of reasons exist for why the above conclusion is somewhat different from the one you might draw from the results of Tanaka (2007): Firstly, the juvenile chimpanzees that took part in Tanaka's experiments were younger—and had experienced touch screen-based tasks at a younger age—than the adolescent chimpanzees that took part in the present study. Secondly, there are various methodological differences between Tanaka's study and

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[3] It needs to be stressed that the experiments presented here did not provide a direct test of Tanaka's (2007) 'critical period' hypothesis.

the present one. Thirdly, although no examples of the black-and-white line drawings used by Tanaka were provided, it is likely that there are important differences between those stimuli and the black-and-white line drawings used here. For example, while all line drawings are inherently more abstract than less degraded stimuli, the impressionistic quality of the line drawings can also affect their perceived level of abstractness.

One important point to note is that, given the small number of subjects involved in the present study—and, for that matter, involved in Tanaka's (2007) study—the conclusions presented above need to be treated with caution. If one does accept these conclusions, however, an interesting question arises: Why do sub-adult chimpanzees outperform adult chimpanzees in the categorisation of pictorial stimuli? Tanaka (2007) proposed one possible answer, hypothesising that the development of (at least high level of) picture recognition relies on experience with pictorial stimuli during a 'critical period' in childhood, which most chimpanzees do not get. However, other possibilities also exist; for example, it has been shown that primates' visual function—including their ability to recognise and identify stimuli—is maximal when they are young (see Andersen et al. 2010), as is the flexibility of an animal's cognition (e.g. Adams et al. 2000; Bartus et al. 1979; Mell et al. 2005; Schoenbaum et al. 2002). Given such, it is equally plausible that sub-adult chimpanzees' superior ability to learn and generalise pictorial categorisations is the result of some combination of the above-mentioned factors. This is not to say, of course, that experience with different kinds of pictorial stimuli at a young age would not be of benefit for the development of (advanced) picture recognition skills; indeed, we are sure it would help. But, while Tanaka's (2007) proposal suggests that experience with pictorial stimuli during a chimpanzee's childhood is essential for effective picture recognition—and therefore categorisation—in adulthood, the alternative possibilities discussed above make no such demand.

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