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AUTHOR CONTRIBUTIONS

CHAPTER 1: INTRODUCTION

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CHAPTER 2: PIGEONS INTEGRATE PAST KNOWLEDGE ACROSS SENSORY MODALITIES

I designed the study and developed the underlying hypothesis. Two students, Martina Stocker and Daniela Bergmann, assisted in collecting the data. I analyzed the data and wrote the first draft of the manuscript. My co-author, Thomas Bugnyar, revised it and gave valuable input on the discussion.

CHAPTER 3: PIGEONS DISCRIMINATE OBJECTS ON THE BASIS OF ABSTRACT FAMILIARITY

I designed the study together with the second co-authors, Anna Wilkinson, and collected as well as analyzed the data. I wrote the first draft of the manuscript and both co-authors, Ludwig Huber and Anna Wilkinson, equally contributed to editing and revising the manuscript.

CHAPTER 4: HAVE WE MET BEFORE? PIGEONS RECOGNISE FAMILIAR HUMAN FACES.

I designed the study together with the second co-authors, Anna Wilkinson, and collected as well as analyzed the data. I wrote the first draft of the manuscript and both co-authors, Ludwig Huber and Anna Wilkinson, equally contributed to editing and revising the manuscript.

CHAPTER 5: HOLOGRAPHY AS A NOVEL TOOL FOR INVESTIGATING 3D-INFORMATION PROCESSING: DISCRIMINATION OF HOLOGRAMS AND REAL OBJECTS BY PIGEONS AND HUMANS

I designed the experiments with input from both co-authors, Ulrike Aust and Michael Steurer. I collected and analyzed the data and wrote the first draft of the manuscript. Ulrike Aust and Michael Steurer revised the manuscript and contributed to the final version of the manuscript.

CHAPTER 6: CONCLUSION

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SUMMARY

Categorization is one of the most fundamental cognitive processes, comprising levels that are characterized by different complexity and which range from route learning to symbolic relations. In empirical animal cognition research, it seems that a priori assumptions about the innate capacity of species to possess 'higher cognition' sometimes prevented the investigation of such abilities in species that are not supposed to be genetically predisposed to show such 'cognitive superiority'. For instance, pigeons were shown to memorize and discriminate pictorial stimuli on the basis of very subtle perceptual features, suggesting that the species' visual perception abilities are outstanding. In contrast, pigeons are hardly considered as a model species to investigate higher forms of cognition and categorization, e.g. functional class formation like found in primate communication systems, although the ecology of pigeons is likely to promote flexible learning of consequences that results from interactions with different external entities.

Based on this mismatch and the considerable lack of even negative results on abstract categorization in pigeons, the experiments presented here aimed to provide novel insights into pigeons' ability to interpret external information on more abstract levels, namely on the basis of functional classes. I found pigeons to abstract class-binding features of stimuli beyond perceptual similarity by referring to information that the birds acquired in the past. More specifically, pigeons were able to discriminate humans and inanimate objects on the basis of previous real-life encounters alone. The birds were also tested in a simulated predatory context, using visual and acoustic cues to predator presence. I found pigeons not only to match predator cues across sensory modalities but also to infer changes in urgency, dependent on previously perceived information and on contextual information.

Additionally to functional class formation in pigeons, I addressed methodological problems in the presentation of pictorial stimuli by testing pigeons and humans on the discrimination of holograms and object-hologram equivalence. Holograms provide a promising alternative to the presentation of pictures as they provide visual information that equals the information perceived with real objects, including information in the 3rd dimension. By this, I tried to provide an alternative methodology to present stimuli that avoids some of the shortcomings and problems in the interpretation of results yielded in experiments that used 2D stimuli.

The combination of novel methods in stimulus presentation and a more unbiased selection of target species in the investigation of different categorization levels represent a conclusive comparative approach to the investigation of factors that led to the evolution of different cognitive abilities. This thesis aims to contribute evidence for pigeons' ability to summarize external information by features beyond physical similarities, by showing context-dependent behavioural flexibility in the birds and by providing very first results on the perception and discrimination of holograms.

ZUSAMMENFASSUNG

Kategorisierung stellt einen der fundamentalsten kognitiven Prozesse zur Reduktion externer Informationen dar und umfasst Ebenen verschiedener Komplexität von schlichtem Auswendiglernen bis zu symbolischer Verknüpfung verschiedener Reize. Innerhalb der empirischen Untersuchung kognitiver Fähigkeiten im Tierreich scheinen anthropozentrische a priori Annahmen über die Komplexität vorhandener kognitiver Eigenschaften einzelner Tierarten zum Teil zu einer Vorauswahl der zu testenden Tierarten zu führen. So wurde beispielsweise gezeigt, dass Tauben ein außergewöhnlich gutes Gedächtnis für präsentierte Bilder besitzen und diese auch anhand von nur äußerst geringfügigen perzeptuellen Unterschieden zuordnen können. Trotz dieser ausgeprägten visuellen Wahrnehmungsfähigkeiten wurden Tauben jedoch kaum hinsichtlich höherer kognitiver Fähigkeiten wie zum Beispiel der Bildung von funktionellen Klassen untersucht. Die Bildung funktioneller Klassen erfordert die Extraktion einer gemeinsamen Funktion, die einzelnen Reizen gemein ist, und führt zur Bildung von Kategorien unabhängig von visuellen oder anderen perzeptuellen Ähnlichkeiten. Dieser Mangel an Untersuchungsergebnissen ist insofern überraschend, als dass die Ökologie dieser Vogelart ein schnelles Lernen von Konsequenzen aus Interaktionen mit verschiedenen Subjekten und Objekten und flexible Verhaltensstrategien durchaus vermuten lässt.

Aufgrund des Fehlens empirischer Evidenz bezüglich komplexerer Informationsverarbeitung bei Tauben zielen die vorliegenden Studien darauf ab, neue Einsichten in die kognitiven Fähigkeiten dieser Vogelart zu liefern, mit besonderem Schwerpunkt auf der Bildung funktioneller Klassen. Die hier präsentierten Ergebnisse zeigen, dass Tauben externe Informationen auf einem bislang unbekannten und komplexen Niveau verarbeiten. Tauben fassten einzelne Reize in Klassen zusammen

indem sie auf vergangene Erfahrungen mit diesen rekurrierten. Im Speziellen waren die hier getesteten Tiere in der Lage, Bilder von einzelnen Menschen und Objekten einzig nach vorhandener Erfahrung mit den realen Menschen und Objekten innerhalb der Voliere zu unterscheiden. Darüber hinaus simulierte ich den Tauben die Anwesenheit eines ihrer relevanten Raubfeinde und testete die Tiere auf die Fähigkeit, Anzeichen dieser Bedrohung über verschiedene Sinnesmodalitäten zu integrieren sowie ihr Verhalten kontextabhängig zu modifizieren. Die hier getesteten Tauben zeigten nicht nur diese Fähigkeit, sondern schlossen außerdem die Dringlichkeit der Bedrohung aus der Sinnesmodalität, in welcher die Raubfeindpräsenz empfangen wurde.

Neben der Bildung funktioneller Klassen stand außerdem die Verbesserung methodischer Ansätze in der systematischen Untersuchung visueller Wahrnehmung und damit verbundener kognitiver Fähigkeiten im Vordergrund. Die zur Zeit bevorzugte Methode bedient sich der Präsentation von Bildern, wobei jedoch etliche daraus resultierende Nachteile in der Interpretation aufgenommener Daten zu berücksichtigen sind. Um diese Nachteile zu umgehen testete ich die Anwendbarkeit von Hologrammen zur wissenschaftlichen Untersuchung von visueller Wahrnehmung und Kognition. Menschen und Tauben wurden auf Unterschiede zwischen Hologramm- und Objektwahrnehmung gestestet (Hologramm-Objekt Äquivalenz) sowie auf die Übertragung von Unterscheidungen zwischen Reizen auf neue Ansichten dieser Reize innerhalb einer Präsentationsart (Hologramm oder Objekt).

Die Kombination aus methodischer Weiterentwicklung und einem Ansatz, der verschiedene Ausprägungen des Kategorisierungsvermögens in einem weiten Artenspektrum untersucht, ermöglicht eine umfassende und schlüssige Erfassung jener Faktoren, die zur Evolution verschiedener Kategorisierungsebenen führten. Die hier vorgestellten Experimente steuern empirische Befunde bei, welche die Fähigkeit von Tauben zeigen, externe Informationen unabhängig von physikalischen Ähnlichkeiten abstrakt zusammen zu fassen. Darüber hinaus zeigen die vorliegenden Ergebnisse, dass Tauben ihr Verhalten in Abhängigkeit des Kontexts, in welchem Informationen empfangen werden, variieren. Dies ist zudem der erste empirische Beleg, dass Tauben in der Lage sind Hologramme wahrzunehmen und diese unterscheiden können.

CHAPTER 1: INTRODUCTION

The present thesis investigates some previously neglected aspects in the formation of functional classes in pigeons (*Columba livia*). In particular, I addressed the integration of acoustic and visual information as well as pigeons' inferring abilities across time in a simulated predatory context in Chapter 2. In Chapter 3 and 4 familiarity-based recognition of inanimate objects and humans beyond perceptual similarity as well as the transfer of real-life experience to the discrimination of pictorial presentations were investigated. In Chapter 5, I will introduce an innovative method to investigate visual perception and categorization that avoids some of the methodological shortcomings of traditional picture presentation techniques. Prior to the presentation of empirical results, I will summarize different levels of information processing with a particular focus on functional classes. Afterwards, I will examine some crucial aspects in visual perception and cognition research that have been a matter of debate the past decades and which had a direct impact on the empirical studies included here.

AN EFFICIENT BOTTLENECK

It is obvious that not all external information available to sensory systems could be processed and weighted on an equal basis. Evolutionarily speaking, a particular piece of information has to compete with other information about being "relevant" enough to be processed and converted into behavioural outputs (e.g. Cook et al., 1990). The attention towards relevant or the ignorance towards irrelevant information as well as the summary of different pieces of external information that require the same behavioural response enables an individual to achieve a reduction of information (Delius et al., 2000a) and increases an individual's inclusive fitness (Hamilton, 1964). Hence, selection favours those individuals that reduce the vast amount of external information in a more efficient way than other individuals and evolution should directly act on all cognitive activities that contribute to the processing and reduction of information and its translation into behavioural outputs.

Both the identification of the information that passes this information-processing bottleneck and the specification of the perceptual and cognitive mechanisms that trigger and accomplish the reduction of information, including mental filtering and inferring mechanisms, can be summarized as **categorization** (Huber, 2000). The perceptual ability to assess external information and the cognitive means to summarize different items into classes highly depend on the focal species and the number of different implementations in the animal kingdom reflects the diversity of life itself (e.g. Marler, 1982; Huber, 1999). Different cognitive levels of categorization are characterized by the degree of abstraction that is needed to mentally manipulate available information and to form classes. The next subsection will summarize mechanisms that may lead to the formation of classes of different complexity by referring to approaches suggested by e.g. Herrnstein, (1990), Zayan & Vauclair (1998), and Zentall et al. (2002).

Different levels of condensing information

If class membership is determined by the memorization of each individually learned object that is linked to a corresponding reinforcer, all informational entities are stored and processed as a "list" without any relations among class members. This process was also labelled as **categorization by rote** (Herrnstein, 1990) or **absolute discrimination** (Vaughan & Greene, 1983). Each memorized item represents its own class and the species-specific (as well as individual-specific) memory capacities literally set the limit of the number of different classes (e.g. Cook et al., 2005; Fagot & Cook, 2006). **Perceptual classes** represent the first level of equivalence formation among objects by building categories that are based on physical similarities, which are greater within than between different classes (e.g. Huber & Lenz, 1993; Huber, 2001). There are basically 3 models to explain mechanisms of discrimination and generalization at that level. First, entire external entities may be mentally stored as intact items. Novel instances are then categorized on the basis of perceptual familiarity to the stored exemplars (*exemplar theory*). Alternatively, individuals may selectively attend to single object cues or to a certain set of features (*feature theory*) that are shared among objects and which may be as complex as subtle perceptual variation between male and female human faces (Troje et al., 1999; Huber et al., 2000; Loidolt et al., 2003). Third, equivalence formation may be based on the abstraction of a prototype of all class members (e.g. Huber & Lenz, 1996). This requires the individual to summarize and represent the general tendency or the average of all instances of class members it has encountered. Thus, *prototype theory* thinks of categorization as the mental computation of the most typical representative of a certain class (Rosch et al., 1976).

If class members share a common consequence that results from an inherent function, **functional classes** are likely to be formed (e.g. Zentall et al., 2008). By this, individuals abstract beyond the perceptual appearance of objects and refer to an innate or learned “knowledge” about the costs and benefits of interacting with these objects. Hence, class members are defined by their function instead of shared physical properties. Typical examples from the animal literature are e.g. *tool* (e.g. in chimpanzees, *Pan troglodytes*: Savage-Rumbaugh et al., 1980) or *food* (e.g. in baboons, *Papio anubis*: Bovet & Vauclair, 2001). Animals may also learn about class-binding common consequences in an operant conditioning paradigm, in which different class members are associated with the same outcome (e.g., reward). If the outcome is the only class-binding feature that connects single stimuli meaning that class members share no additional, intrinsic relationship, class formation is said to be based on acquired equivalence (Urcuioli, 2001). Hence, in contrast to rote learning (where each item and the reward is it's own class and item-reward relations learnt separately), classes formed by acquired equivalence are based on training during which the reward defines class membership. However, the difference between both might well dissolve as training proceeds and the common reward of separately learnt items might result in the formation of classes based on the reinforcement. Whether the distinction of categorization based on functional as opposed to acquired equivalence indeed makes sense is, still a matter of debate.

Animals have also been shown to form **relational classes**, although species differences are remarkable (Vasconcelos, 2008). The formation of classes of items by a set of features that refer to relationships between single objects has been investigated under several aspects, e.g. *sameness/difference* (e.g. in monkeys and pigeons: Wasserman & Young, 2010; Wright & Katz, 2006), *transitive inference* (e.g. in birds: Lazareva & Wasserman, 2006; Mikolasch et al., 2012; in monkeys: Treichler & van Tilburg, 1996; Maclean et al., 2008 and in fish: Grosenick et al., 2007) or *inference by exclusion* (e.g. in dogs: Erdöhegyi et al., 2007; Aust et al., 2008 and in monkeys: Petit et al., 2005; Sabbatini & Visalberghi, 2008). Despite profound empirical evidence for some species being able to recognize such first-order relationships, simpler explanations in terms of e.g. stimulus avoidance must always be considered as an alternative mechanism underlying discrimination performance (e.g. Schloegl et al., 2009). Second-order relationships, which are relationships between relationships, require the animal to transcend the first-order relationship between single stimuli and to make inductive inferences by judging the equivalence of relationships (e.g. Zentall et al., 2008; Huber, 2010). Until recently, only apes that were previously trained in symbolic categorization succeeded in matching stimulus pairs according to the relation between single stimuli (Premack, 1983; Thompson & Oden, 1996) but approaches that used larger sets of stimuli for the representation of particular relationships seem to challenge the exclusiveness of this cognitive ability in apes (Cook & Wasserman, 2007). From here, it is only a small step to *analogical reasoning***,** which is defined as the ability to judge the equivalence of relationships between two sets of stimuli at a level that extends beyond sameness and difference (see Pearce, 2008). The most abstract form of categorization that only humans use is characterized by the symbolic reference to external information (**symbolic classes**), which is expressed in the usage of language (Huber, 2010).

Functional classes

Empirical studies in the present thesis will mainly refer to the middle range of complexity in categorization, namely functional classes. Animals naturally respond to functional categories in a seemingly effortless manner. In nature, functional classes are supposed to be based on consequences that result from interactions with external entities. Typical examples of how functional classes are expressed in behavioural outputs include the recognition of conspecifics or heterospecifics. These classes are most commonly based on the recognition of exemplars. This means that an individual classifies class members by features that are provided by the recognized class member itself. In the case of conspecific recognition, functional classes are often defined by kinship (e.g. Rendall et al., 1996; Aubin & Jouventin, 1998; Leclaire et al., 2013; for review see also e.g. Beecher, 1988; Hepper, 1991), mating partners (e.g. Bonadonna & Nevitt, 2004; Magurran & Ramnarine, 2004), territory neighbours (e.g. Müller & Manser, 2007; Van Dyk & Evans, 2007) or even by more abstract features like familiarity (e. g. Coffin et. al, 2011; Schell et al., 2011). In contrast, heterospecific recognition seems to be particularly advantageous in the context of predation avoidance (e.g. Magrath et al., 2009; Cornell et al., 2012) or for domesticated animals that frequently interact with humans (e.g. Taylor & Davis, 1998; Racca et al., 2010; Proops & McComb, 2012). Several species are capable of both recognizing individual differences and subgroups of conspecifics and heterospecifics according to, for example, one of the above class-binding features. For instance, pigeons were shown to attend to, memorize and discriminate conspecifics (Nakamura et al., 2003) on the basis of static visual features but also on the basis of previous encounters (Wilkinson et al., 2010). In terms of heterospecific recognition, pigeons also categorize humans depending on previously encountered hostile or friendly behaviour (Belguermi et al., 2011).

Another aspect of functional class formation that gained considerable attention is the inference and categorization of external events by labels. These labels are required to have a distinct physical structure and to be unambiguously linked with the actual class member (the eliciting event). Hence, the individuals that perceive these labels also form categories according to the common function or consequence of class members, i.e. events that elicit behavioural responses. But, in contrast to the formation of functional classes by exemplars, the external events are inferred from cues that are perceived in absence of any perceptual cues provided by the eliciting event itself. For instance, the inference of predator presence or of threatening events by means of labels, namely functionally referential signals (e.g. alarm calls: Marler et al., 1992; Blumstein, 1999; Seyfarth et al. 2010) provided fascinating insights into highly sophisticated interpretative abilities of perceivers in various species (e.g. behavioural responses in dependence on the presence or composition of the audience,

audience effects: Vignal et al., 2004 ; Ridley et al., 2007 or context-related behavioural responses: Charlton & Reby, 2011; Candiotti et al., 2012). Regarding highly flexible behavioural responses that vary with the context in which a piece of information is perceived, most studies focussed on species that possess both sides of information transmission, signal production and perception. Hence it remains difficult to evaluate whether these cognitive abilities are domain specific for communication or represent more general abilities that are shared by species that form functional classes but do not possess elaborate signalling traits. Indeed, empirical evidence suggests that species, which do not produce alarm calls link predator presence and heterospecific alarm calls but that these links are learned associatively and do not represent the same complexity found in highly vocal species (e.g. Lea et al., 2008). In general, the cognitive abilities that led to the inference of events by labels are of high interest in terms of the exact level of categorization. Whether functional class formation is sufficient to explain elaborate interpretative abilities in some species or whether more sophisticated capacities, like the formation of relational or symbolic classes or mental representations are involved, remains to be clarified.

Because the remainder of the present thesis will mainly focus on visual perception, although the necessity of a cross-modal approach will not be entirely neglected, the next section will briefly summarize what we already know about visual categorization capacities in the model species investigated here, namely the pigeon.

EMPIRICAL STUDIES ON PIGEONS' CATEGORIZATION ABILITIES AND THEIR IMPLICATIONS

For several reasons, pigeons are among the most promising species to investigate visual categorization mechanisms in general and the formation of functional classes in particular. These birds combine highly sophisticated perceptual capacities with an ecology that promotes the evolution of flexible behavioural strategies regarding fast and flexible learning abilities as an urban-living species in an environment that might change rapidly (e.g. Levey et al., 2009; Belguermi et al., 2011; Lee et al., 2011), although the effect of habitat complexity on cognitive traits, like e.g. innovation rate, is still a matter of debate (Levebvre & Sol, 2008; Overington et al., 2011). . Furthermore, as a prey species, pigeons are evolved to recognize potential threats reliably as well as to promptly respond to predator presence (e.g. Ingle, 1968; Ydenberg & Dill, 1986; Lind & Creswell, 2005).

Pigeons lack advanced vocal communication capacities (Sisson, 1968; Rashotte et al., 1975), therefore representing an ideal model species to investigate cognitive abilities that were previously thought to have evolved only in highly vocal species. Furthermore, studies on pigeons' discriminative abilities contributed extensively to our current knowledge about non-human categorization (e.g. Cook et al., 1990; Huber, 1999; Zentall et al., 2008), providing a profound empirical basis. Despite this seems somewhat counterintuitive, pigeons also represent a promising comparative reference to visual information processing in humans. Although birds and mammals are evolutionarily separated by at least 310 million years and diverged in the evolution of their perceptual systems, both species are highly visual (Kumar & Hedges, 1998; Delius et al., 2000). Nevertheless, pigeons and humans are phylogenetically sufficiently separated to prevent over-interpreting their cognitive abilities, as humans often tend to do with closer related species like e.g. nonhuman primates (Lea, 1984).

The following paragraphs will focus on some methodological aspects, namely the use of "natural" and "artificial" stimulus classes in visual categorization, the discrimination and categorization of pictorial information and the potential of cross-modal approaches in pigeon research. These methodological issues were crucial for the design of the studies on the formation of functional classes by pigeons that will be presented subsequently.

Natural categories and artificial stimuli

Starting with the classical experiment of Herrnstein & Loveland (1964) in which pigeons were found to discriminate pictures on the basis of whether humans were depicted or not, researchers successfully continued to provide evidence of categorization of natural stimuli like e.g. trees (Herrnstein et al., 1976), oak leaves (Cerella, 1979), birds vs. other mammals (Bhatt et al., 1988), cats, flowers, cars and chairs (Wasserman et al., 1988), food vs. non-food (Watanabe, 1991) and many more. With an increasing interest in the features that triggered correct discrimination, scientists became aware of problems resulting from natural variation within classes. As stated by Huber (1999), natural variation is one of the most fundamental principles of evolution and deciding whether an encountered object is a member of a certain class or belongs to another class is crucial for categorization, especially as most natural objects are not only complex, but also variable in their appearance (depending on the viewing angle, visual access, light conditions, distance, etc.). Furthermore, a single item may well be a member of different classes and the linkage between items and attributed class membership is supposed to be highly flexible depending on the receiver's perceptual abilities, ontogenetic experiences, memory capacities and contextual conditions. Most of the "informational packages" that are received in natural environments are constituted by polymorphous features, of which not a single one may be identified to be necessary or sufficient for the definition of class membership (Ryle, 1949). Especially with regard to functional classes, it seems reasonable to assume that different object properties contribute to their function and that the context in which the information is received adds to the interpretation of the perceptual input and determines the behavioural output. If natural functional classes like *food* or *predator* have been part of the species evolutionary history, the subject's ability to identify instances of relevant classes and the corresponding behavioural response is likely to be influenced by the level of variation within that functional class (Huber, 2000). This co-variation between perceptual abilities, learning capacities and natural variation in external entities might be an additional reason for the apparent difficulty that animals have in learning artificial polymorphous classes (Lea et al., 2006). Hence, if correct classification depends on the correlation of several features, their combination and relative frequency (Lea & Harrison, 1978; Cerella, 1982), it will be hardly possible to identify all features that make up a category as perceived by the individual (Fetterman, 1996). Even when response rates of individuals correlate with some predefined cues, like e.g. colour (Huber et al., 2000) it remains impossible to rule out other features that may have been included in the polymorphous rule as well and to which individuals may have paid attention (von Fersen & Lea, 1990). A recently proposed approach integrates these difficulties and proposes a "modified feature theory" that is polymorphous itself and combines previously separated aspects of categorical abstraction, flexibility and attention switching between different levels of features (Huber & Aust, 2011).

An alternative approach is provided by experiments that use artificial stimulus classes. Within these, class membership can be determined on the basis of well-controlled compositional features and animals' response patterns may give us a glimpse into whether those features could be perceived and used to accomplish the task. A classic example of how pigeons are able to use predefined topological and general aspects of form to distinguish “A”s and “2”s in different typefaces was provided by Morgan et al. (1976). Other studies also used alphabetical stimuli (Lea & Ryan, 1983; Blough, 1985), cartoon figures (Cerella 1980), line drawing of the human face (Huber & Lenz, 1993, 1996), different geometrical stimuli (Jitsumori, 1993) or dot patterns (Watanabe, 1988). One way to model polymorphous classes is the “m-out-of-n” feature rule (Lea et al., 2006). According to this rule, classes are defined by “n” features that have binary dimensions (present/non-present) and class membership is constituted by the presence of at least m features (usually, “m” should be greater than “n/2” in all exemplars). However, although artificial classes clearly provide better control over available features than do natural classes, they also have disadvantages. For example, if categories made of such impoverished exemplars are characterised by only few, non-correlating cues and/or if the structure of feature compositions is represented in an unnatural manner, e.g. due to equal frequencies of feature combinations, then they might not match animals’ naturally applied strategies. In other words, animals may have to first learn to attend to a level of simplicity they do not encounter normally, although previous studies suggest that pigeons could also use a more flexible sum rule instead of a somehow rigid “m-out-of-n” feature rule (Huber & Lenz, 1993).

Combining the use of natural stimuli that reflect the complexity and variability usually encountered in natural classes and that of artificial stimuli whose feature content can be well-controlled, the synthetic approach (Huber, 2001) integrates the advantages of both while avoiding their main disadvantages. Based on pigeons’ ability to discriminate female and male human faces (Troje et al., 1999), Huber et al. (2000b) used the synthetic approach to investigate the stimulus properties that underlay the birds’ reliable categorization of human faces. First, the authors extracted the visual information that distinguished both stimulus classes most accurately (resulting in three principle components that mainly represented colour, intensity differences between parts of the faces and shading). Second, they modified pictures of female and male human faces along these dimensions and tested the birds for discrimination of these modified stimuli. Pigeons' discrimination was indeed found to correlate with the extracted components. The capture of potential discriminative features by principle components that reliably separated both categories of stimuli and the modification of these components provided remarkable insight into the mechanisms that guided pigeons categorization and gave rise to additional studies that proved a previously unknown flexibility and complexity of pigeons' visual discrimination abilities (for review see Huber, 2003).

In conclusion, natural stimuli provide good representations of feature combinations that the birds are naturally confronted with but their exact nature is hard to control and single features or feature combinations that trigger pigeons' categorization are hard to identify. The structural organisation of artificial stimuli is easier to control but may not resemble the conditions under which the birds' cognitive and perceptual abilities evolved. If mechanisms of discrimination are addressed, the synthetic approach is certainly the best choice. However, if the research focus lays on the cognitive requirements that underpin the formation of natural functional classes and the cognitive challenges under which successful categorization evolved and can still be observed, stimuli should be used that represent natural classes and whose feature content was not systematically varied.

The use of pictures in visual perception and discrimination research

Pictures do not contain all physical information that is perceived with real objects and only represent impoverished versions as compared to real-life entities (Lea, 2010).

Hence, from a physical point of view, it seems highly unlikely that pictures appear ecologically valid and realistic to animals, especially in portraying real-life objects or categories (for reviews see D'Eath, 1998; Beilin, 1999; Bovet & Vauclair, 2000; Fagot, 2000). Whereas a photograph is a point-to-point recording of the intensity (i. e., the square of the amplitude of the electric field) that illuminates each particular point on the film (including repeated recordings in colour photography that resemble human spectral maxima), the light that is reflected from real objects also carries phase information. Wavelength and amplitude of the light are captured in pictures, but phase information is lost and this loss results in deprived directional information, namely a lack of the 3rd dimension. Furthermore, photographs are always impoverished representations of real objects because they lack additional cues like acoustic, olfactory or (in the case of depicted conspecifics or heterospecifics) behavioural features, like complex patterns of mating behaviour or recipient-directed hostile or friendly behaviour that might influence recognition and discrimination. Especially for birds, anthropomorphic assumptions about birds' vision hampered the progression of knowledge about visual perception (and probably also learning abilities). An example of how birds' visual perception in general was misinterpreted due to anthropomorphism is summarized by Weisman and Spetch (2010). The sexual dimorphism in passerine birds was highly underestimated until Eaton (2005) considered the birds' physiology and included UV plumage reflectance into the investigation of phenotypic differences between sexes. Considering the latter in the analysis, 125 out of 139 bird species turned out to be sexually dimorphic and had to be reclassified. This illustrates the risk of neglecting the differences between species' perceptual abilities. The use of picture technology that is adjusted to humans (Bovet & Vauclair, 2000; Delius et al., 2000) bears a similar risk regarding the interpretation of birds' performances in discrimination and recognition tasks. Especially negative results (in which birds failed to discriminate pictorial presentations of real-life entities) are hard to interpret. With these, it remains unclear whether the birds were unable to discriminate the stimuli because the pictures lacked stimulus features that were present in the real objects and whether they would have succeeded if presented with real-life objects (as suggested by Dittrich et al., 2010). Positive results, on the other hand, do not prove that the birds used the same discriminative features as would humans (Watanabe, 2010) and the identification of these features is problematic.

Although some experiments convincingly showed that pigeons refer to real-life experience with objects in the discrimination of pictures thereof (e.g., Aust & Huber, 2006, 2009), categorization of pictures alone does not clarify whether the discriminative features are the same as those that might be used in the categorization of real objects. There are three approaches that may provide promising accounts to the problem of picture-object correspondence. First, as Weisman and Spetch (2010) suggested, a transfer test from real objects to pictures may reveal whether a change in the presentation mode impairs categorization. However, if pigeons succeed, that does not necessarily prove that birds see pictures as representations of objects (instead they may have used simple 2-D features present in both the object and its picture, and/or may have confused pictures and objects). Second, similar to the approach used in the complementary information procedure by Aust and Huber (2006), pigeons may be trained to discriminate pictorial representations of objects they encountered in real-life. More specifically, Aust & Huber (2006) used pigeons' pre-experience with humans to test the birds' transfer of recognition to pictorial presentations of only parts of humans. For this purpose, the authors trained pigeons with photographs of incomplete human bodies and tested them with the previously missing parts (hands or heads). The pigeons' successful categorization of test stimuli relied on their spontaneous recognition of parts that usually belong to humans, thus proving the existence of some mental representations of complete humans in the birds. Hence, if the reference to previous experience provides pigeons with the class-constituting feature (e.g. the visual appearance of complete entities or a common consequence) and pigeons were able to recognize objects in pictures, then birds that experienced this common consequence should correctly classify novel pictures. Birds that lack this kind of experience should fail to discriminate pictures of novel category exemplars in a transfer test. Third, as it is difficult to overcome short-comings in the production and presentation of pictures (Delius et al., 2000), future experiments should aim at developing alternative methods in stimulus presentation that are adapted to e.g. avian visual perception and minimize the reduction of transmitted information (as compared to picture presentations).

Pigeon research beyond the visual domain

Although pigeons have been studied extensively, the proportion of studies that include other sensory modes than the visual is surprisingly small. For instance, there are only few studies that investigated pigeons' categorization abilities in the auditory domain, although it is known that pigeons possess the respective physiological abilities. Heffner and Heffner (2007) showed that pigeons perceive acoustic stimuli in a range from 150 Hz to 5.8 kHz at a sound pressure level of 60 dB. Lewald (1987) gave indirect evidence for the ecological importance of the auditory mode in pigeons by proving that the birds are able to locate sounds with high accuracy, comparable to the abilities of highly specialized owl species. The importance of auditory cues in pigeons' natural behaviour was further supported by a study on Crested pigeons (*Ocyphaps lophotes*), another genus in the Columbidae family. These birds were found to use a mechanically produced flight noise, namely wing whistles, to infer a nearby threat. They generate wing whistles that vary in tempo according to whether the bird took off in alarm or not (Hingee & Magrath, 2009) and conspecifics eavesdrop on these cues and infer the urgency of the causing threat.

Concerning classification in the auditory domain, Porter and Neuringer (1984) demonstrated that pigeons could discriminate between different styles of classical music, and that they could transfer this discrimination to similar, novel pieces of music. Partan et al. (2005) combined sensory information into multimodal signals and compared female responses to displayed male visual and acoustic courtship behaviour. Somehow unsurprisingly, females' behavioural responses were highest when visual and acoustic information were integrated simultaneously. However, also acoustic cues alone resulted in increased response behaviour of females relative to response behaviour to mute video presentations of males.

Multimodal cues and cross-modal information in general have been investigated in a variety of taxa including mammals (e.g. Proops et al., 2009, Sliwa et al., 2011), birds (e.g. Baptista, 1978; Todt & Fiebelkorn, 1979; Beletsky, 1983), amphibians (e.g. Lewis et al., 2001; Narins et al., 2003) and insects (e.g. Elias et al., 2003). However, their importance has been emphasized mainly in the investigation of recognition and communication in the social context (for review see Partan & Marler, 2005; Tibbetts & Dale, 2007; Ryan et al., 2009; Slocombe et al., 2011) with only few exceptions (e.g. Giurfa et al., 2001). Regarding the receiver's side, it is categorization that underlies behavioural outputs and given the importance of this mental process in structuring the external world, the mechanisms involved may not be restricted to a certain sensory mode or the social context. The integration of different sensory modalities provides a promising approach to investigating the level of abstractness at which pigeons (and other animals) are able to categorize (e.g. whether pigeons perceive the principle of "sameness" across perceptually very different stimuli and can hence form relational classes; Huber, 2010). Only because pigeons are highly visual, we might indeed have underestimated their categorization abilities by restricting empirical research mainly to the visual domain.

ONE STEP BEYOND – AIMS AND SCOPE OF THE THESIS

The experiment presented in **Chapter 2** tested the pigeons' ability to interpret information about predator presence across sensory modes by combining information in the visual and the auditory domain. The birds were presented with stuffed models and territory calls of one of their main predators, the common buzzard (*Buteo buteo*), and with a control stimulus (a pheasant, *Phasianus colchicus*) in a habituation/dishabituation paradigm (Eimas, 1971). The analysis of the birds' behavioural responses was expected to shed light on whether pigeons are able to infer the referent of the signal and the encoded urgency across sensory modes in a context-sensitive way (by referring to past knowledge). If the birds can abstract the functional class "predator" and form relations between buzzard stimuli cross-modally, identical dishabituation stimuli should result in different responses, depending on whether they are classified as transmitting the same or novel (different) information about a predatory threat.

Also, **Chapters 3 and 4** deal with functional classes, however, with categorization on the basis of abstract "familiarity". Both studies investigated pigeons' abilities to transfer their real-life experience with inanimate human-made objects (Chapter 3) and human faces (Chapter 4) to pictorial presentation thereof. After the acquisition phase in which the birds learned to which discriminative feature they should attend, they had to transfer the discrimination to novel instances of familiar and unfamiliar inanimate objects or humans, respectively. A subject group that never saw any of the objects served as a control to rule out any perceptual features that would enable the birds to discriminate the objects. The only possible way to master the test was to memorize previous encounters with the real objects or faces and to transfer this knowledge to the pictures of these stimuli.

Class-level recognition among perceptually similar entities or items (e.g. conspecifics) as was examined in Chapters 3 and 4 represents a more sophisticated level of categorization than the mechanisms underlying the recognition of a predator vs. a non-predator (Chapter 2), and is supposed to have evolved especially in social species. According to the social intelligence hypothesis (Whiten & Byrne, 1997) advanced cognitive abilities like conspecific recognition on a sub-class level was promoted by challenges posed by the social structure of species. However, especially for animals that frequently interact with humans, heterospecific recognition of human individuals should be equally beneficial. Previous studies found evidence for the discrimination between humans by pigeons (Belguermi et al., 2011), but attempts to find evidence for the recognition of familiar humans by facial cues when presented as pictorial stimuli have failed so far (Dittrich et al., 2010).

Whereas familiar humans might be relevant and hence memorized, this is not that obvious for inanimate objects. Thus, we further divided the familiar objects into those that served a certain function in the aviaries (“relevant”) and those that were just present without serving any obvious function (“irrelevant”). Watanabe (1992, 1996) showed that different brain structures are activated depending on the relevance of presented stimuli and the experiments presented in Chapter 3 investigated if additional “relevance” of objects might also have an impact on the formation of functional classes. Furthermore, both chapters also report evidence for picture-object correspondence because the discriminative feature had to be transferred from the individuals' real-life experience and was not an a priori feature that was inherent in the object.

Chapter 5 aims at providing methodological progress in visual categorization research in pigeons (and other animals) by developing and testing a novel method of stimulus presentation that avoids most shortcomings of pictorial stimuli as well as the disadvantages of real objects. For this purpose, holograms were used in a comparative approach. Holograms provide a number of advantages compared to both picture and real object presentation. They provide full 3D-information and may thus help to understand the impact of the third dimension on object discrimination and categorization. The advantage of holograms over real objects is the possibility to flexibly manipulate a wide variety of physical features more easily than can be done with objects. Furthermore, holograms are less susceptible to physical changes over time, e.g. damages, and thus guarantee for equal stimulus appearances also over longer experimental periods. For these experiments, we used a completely novel apparatus, the Multi-Stimulus Box (Steurer et al., 2012), which was developed for the presentation of 2D and 3D stimuli as well as for the presentation of holograms to humans and non-human animals.

Two groups of pigeons and two groups of humans were trained to discriminate either holograms or real objects. Afterwards, all groups were tested for transfer to the presentation mode they had not been trained in, meaning that subjects trained with holograms were tested with real objects and vice versa. Transfer of discrimination (hologram-object and object-hologram) was compared within each species to evaluate the correspondence of different kinds of stimulus presentation (Weisman & Spetch, 2010). Additionally, performance regarding the discrimination of holograms or real objects was compared between species. A follow up test addressed generalization to novel viewing angles in pigeons and humans, namely rotational invariance, which is supposed to be especially relevant for highly mobile animals such as birds and primates.

Chapter 6 summarizes the empirical findings presented here and draws conclusions on how the results contribute to present knowledge about categorization in pigeons in general and the formation of functional classes in particular.

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CHAPTER 2: PIGEONS INTEGRATE PAST KNOWLEDGE ACROSS SENSORY MODALITIES

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ABSTRACT

Advanced inferring abilities that are used for predator recognition and avoidance have been documented in a variety of animal species that produce alarm calls. In contrast, evidence for cognitive abilities that underpin predation avoidance in nonalarm-calling species is restricted to associative learning of heterospecific alarm calls and predator presence. We investigated cognitive capacities that underlie the perception and computation of external information beyond associative learning by addressing contextual information processing in pigeons, *Columba livia,* a bird species without specific alarm calls. We used a habituation/dishabituation paradigm across sensory modes to test pigeons' context-dependent inferring abilities. The birds reliably took previous knowledge about predator presence into account and responded with predator-specific scanning behaviour only if predator presence was not indicated before or if the perceived level of urgency increased. Hence, pigeons' antipredator behaviour was not based on the physical properties of displayed stimuli or their referential content alone but on contextual information, indicated by the kind and order of stimulus presentation and different sensory modes.

Keywords: *Columba livia*, contextual understanding, cross-modal recognition, pigeon, predator recognition, response urgency

INTRODUCTION

Several vertebrate species have been shown to denote external events in their vocalizations and previous studies have revealed sophisticated inferring abilities of receivers that go beyond mere associative processes (reviewed in e.g. Evans, 2002; Seyfarth et al., 2010; Fitch & Zuberbühler, in press). The encoded referents of such signals may range from broad to very specific contexts and seem to induce mental representations of the external events eliciting them. For instance, rhesus monkeys, *Macaca mulatta*, seem to differentiate food call types by their external referents rather than by their acoustic features (Hauser, 1998), chickens, *Gallus gallus domesticus*, seem to take past knowledge into account during foraging (Evans & Evans, 2007) and several alarm-calling species extract information from both the signal itself and the context in which it is uttered (Rainey et al., 2004; Ridley, et al. 2007; Zuberbühler, 2010). Hence, receivers do not have an automatically triggered behavioural response but seem to take contextual knowledge into account. These sophisticated cognitive abilities have been reported for species that show both sides of information transmission: signalling and receiving (Arnold & Zuberbühler, 2008; Ouattara et al., 2009a, b). However, there is by no means a representational parity between signalling and receiving, nor is ‘meaning’ in a linguistic sense transmitted between signaller and receiver (Fitch & Zuberbühler, in press). How different the cognitive requirements of signallers and receivers might be is especially apparent in the alarm-calling behaviour of many species. ‘Functionally referential’ signals are often produced in threatening situations and are thought to decrease the level of uncertainty about a nearby threat in receivers (Seyfarth et al., 2010). They are highly context specific, show an unambiguous physical structure and trigger the same response in receivers as the actual event (e.g. Marler et al., 1992). However, while there is debate about whether the signaller intends to inform (Cheney et al., 1996; Cheney & Seyfarth, 1990; Tomasello & Call, 1997; Rendall et al., 2000) and about the exact definition of the information content (Rendall et al., 2009), there is growing evidence for elaborate inferring mechanisms in receivers (Fischer, 1988; Rendall et al., 1996; Zuberbühler et al., 1999).

Most studies so far have focused on animal species that produce alarm calls in the context of predation and thus possess cognitive skills that are involved in both signalling and perceiving information about predator presence. There is evidence that also some nonalarm-calling species such as lacertid lizards, *Oplurus cuvieri cuvieri* (Ito & Mori, 2010), iguanian lizards, *Amblyrhynchus cristatus* (Vitousek et al., 2007) and dik-diks, *Madoqua guentheri* (Lea et al., 2008) associate heterospecific vocal cues with predator presence and that they eavesdrop on these signals to avoid predation. However, whether nonalarm-calling species are also able to decode the referent of the signal and to infer the event that elicited it remains unknown. In general, nonalarm-calling species may provide a promising basis to address questions concerning cognitive mechanisms that underpin call interpretation in highly vocal species. Specifically, we can test whether advanced interpretation mechanisms found in alarm-calling species are specialized cognitive abilities that are used for communication or whether they represent more general inferring abilities that are not domain specific.

Pigeons, *Columba livia*, are prey for a variety of ground and aerial predators in rural and urban habitats and thus represent an ideal model species to investigate antipredator strategies. The vocal repertoire of pigeons is relatively limited and does not include specific alarm calls (Sisson, 1968; Rashotte et al., 1975); however, pigeons are renowned for their extraordinary visual discriminative abilities and memory capacities (Vaughan & Greene, 1984; Cook et al., 1990; Huber et al., 2000; Aust & Huber, 2006; Stephan et al., 2012). Although past research on pigeons has mainly concentrated on visual tasks, acoustic playback experiments with pigeons provide a promising means to investigate the birds' inferring abilities. First, the perception of auditory cues to predator presence is less costly (in terms of searching time) than visual vigilance and predators might be detected faster by auditory cues than by visual ones. None the less, costs may also arise from misinterpretations regarding elicited predator attention (Ingle, 1968) or energetically costly antipredator behaviour (Ydenberg & Dill, 1986), although the exact determination of costs resulting from antipredator behaviour is problematic (Lind & Cresswell, 2005). Consequently, evolution should favour individuals that reliably detect predators also in the auditory domain. Second, pigeons might infer different information from predator cues in sensory modes other than the visual in terms of urgency. For instance, pigeons may interpret both buzzard, *Buteo buteo*, calls and a buzzard to indicate buzzard presence but also obtain different information from the two signals about the distance or the visibility of the predator. Hence, the two signals may elicit different behavioural responses to avoid predation depending on the level of urgency that is perceived by the birds. This difference in response to cues in different sensory modes could provide further insight into the relationship between urgency-based and predator-specific antipredator behaviour. While the majority of studies have focused on the effects of urgency on call production (Macedonia & Evans, 1993; Manser, 2001; Manser et al., 2002; Templeton et al., 2005), only a few have addressed the receiver's behavioural output in response to the perceived level of urgency (Warkentin et al., 2001; Randall & Rogovin, 2002; Leavesley & Magrath, 2005) or the impact of presentations across sensory modes (Slocombe et al., 2011).

We tested pigeons for cross-modal contextual understanding (using visual and acoustic cues). Notably, they should not merely react to physical signal properties but also take previous information about predator presence into account. For this purpose, we used stuffed models of a common buzzard as a visual predatory stimulus and a pheasant, *Phasianus colchicus*, as a control stimulus in a habituation/dishabituation paradigm (Eimas et al., 1971). In addition, acoustic playbacks of buzzard calls served to simulate predator presence at a different level of urgency to the pigeons. Playbacks of pheasant calls served as a control stimulus in the auditory domain. Specifically, we predicted pigeons would dishabituate more strongly to buzzard models and buzzard calls whenever pheasant stimuli were displayed before the buzzard stimuli. If buzzard models are presented first, the birds should show no response to buzzard calls. In contrast, if buzzard models are perceived as being more urgent than buzzard calls, pigeons should show unambiguous dishabituation to visual models.

METHODS

Subjects and housing

We tested 60 adult pigeons in pairs (*N*=30) from March to June 2011. All birds were colour-ringed and individually identified. The pigeons were housed in flocks of 8–16 individuals in outdoor aviaries at the University of Vienna that were equipped with perches, nestboxes and water dispensers. Water and grit were freely available whereas food was provided indoors during visual discrimination tasks independent of the present study and over the weekend. Previous experience with predator encounters (acoustic, visual or physical) was estimated by evaluating the subject's ontogenetic history. Only birds that had been either free flying in the past or had visual access to the outdoors (and thus to predatory attacks on wild conspecifics) participated in the present study. The occurrence of raptor attacks in the direct vicinity of the aviaries has been confirmed (C. Stephan, personal observation), although the exact frequency of predator encounters remains unknown. All subjects that participated in the experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act – TSchG, BGBl. I Nr.118/2004). Furthermore, as the present study was strictly noninvasive and based on behavioural observations, all experiments were classified as nonanimal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

Stimuli

We used representations of two roughly equally sized bird species in two sensory modes, namely stuffed models and territory calls. We used the common buzzard as a raptor species and a pheasant as a control stimulus. The buzzard as the critical predatory stimulus was chosen with regard to its geographical distribution and habitat use during hunting, both enhancing the likelihood that focal pigeons have had prior experience with it. Within the visual domain we controlled for size, similar plumage coloration and body orientation between a buzzard and a pheasant model. This served to investigate whether pigeons could also discriminate between perceptually similar models of two different bird species. However, as the focal question addressed context-dependent information processing across sensory modes with a predator, we could have theoretically used any nonthreatening object as a control stimulus. Both visual stimuli were presented separately in a cardboard box, and we controlled the duration of presentations by opening or closing a sliding door (Fig. 1).

Acoustic stimuli were obtained from an online source (http://www.xeno-canto.org) and identified as uttered in territorial behaviour. We used territory calls of two different buzzards and two different pheasants and presented them alternately to the different dyads of a group to reduce the effect of pseudoreplication. A single buzzard call lasted approximately 0.7 s and was naturally produced in a sequence of three subsequent calls, resulting in an overall duration of about 5 s (including breaks of approximately 1.4 s each). The pheasant's call lasted 0.3 s and was not naturally produced in a sequence. We repeated pheasant calls three times (including breaks of 1 s) and created sequences of about 3.5 s to expose the birds to a similar number of calls (for examples of spectrograms of acoustic stimuli see Fig. A1 in the Appendix). We did not manipulate the length of single territory calls as these reflect natural variation and provide perceptual features that may enable pigeons to discriminate between a predator and a nonpredatory stimulus. To modify sequence length we used PRAAT DSP package v. 5.1.29 (Boersma & Weenink, 2005). All playbacks were broadcast using an iPod Nano (fifth generation) connected to a speaker amplifier (ION Block Rocker, 70 Hz–50 kHz ±3 dB).

Figure 1 Visual stimuli. Stuffed models of (a) a common buzzard (*Buteo buteo*) and (b) a pheasant (*Phasianus colchicus*). Both visual stimuli have been presented to the pigeons in a cardboard box, (c).

Behavioural variables & data analysis

We conducted an observational study prior to the playback study to encode the pigeon's behavioural repertoire in a variety of contexts. We did not restrict the definition of behavioural variables to disturbing or threatening events as knowledge about the pigeon's natural response to predators is scarce and the reaction of captive pigeons to simulated predator presence is largely unknown. The full description of the subject's activity pattern amounted to 17 variables (for detailed information see Table A1 in the Appendix). One of these variables was exclusively observed in the context of simulated predator presence (predator-related scanning behaviour) and not during the observational period, in which the birds did not encounter predator models or real predators. The birds also did not show this kind of scanning behaviour to pheasant stimuli. Hence, we had to add the description of this specialized behaviour after the first habituation trials. Although we did not expect any information transfer, for instance 'functionally referential' signalling between individuals, the exact influence of surrounding conspecifics on the behaviour of the focal subject was beyond our knowledge. Thus, to prevent any impact of audience effects on the bird's reaction to displayed stimuli (e.g. the absence of produced signals owing to the absence of potential receivers) and to reduce stress responses from separation, all pigeons were tested in pairs. For this purpose, pair partners were determined during the observational period. In all cases in which no affiliated pigeon could be identified, we assigned nonagonistic conspecifics from the same aviary. The bird's behaviour was recorded during experiments using a video camera (Sony DCR-SR55). The first subject of one pair that altered its behaviour in response to the dishabituation stimulus was analysed as this guaranteed stimulus-directed response behaviour and excluded response patterns that were elicited mainly in reaction to the behaviour of the conspecific. We analysed the videotapes in a frame-by-frame analysis using the Solomon Coder beta v. 11.06.01 (A. Peter, www.solomoncoder.com) to quantify the bird’s behavioural response. The occurrence and duration of each of the defined variables were recorded and analysed.

Procedure and set up

We applied a habituation/dishabituation paradigm to assess pigeons’ ability to infer predator presence across sensory modes and contexts. All pairs of pigeons were assigned to six different groups according to the kind and order of stimulus presentations during habituation and dishabituation (Table 1), resulting in a total of five pairs per group. Pigeons of groups 1 and 2 were presented with pheasant cues in the habituation phase and with buzzard cues in the dishabituation phase. The stimuli were presented in the same sensory mode within groups (group 1: visual; group 2: auditory). Both groups served to clarify whether pigeons are perceptually able to discriminate both stimulus species within a sensory mode. Groups 5 and 6 were also presented with pheasant cues in the habituation phase and with buzzard cues in the dishabituation phase but in different sensory modes within groups. Hence, these groups tested for behavioural responses to referential and perceptual changes in the information that was provided. Groups 3 and 4 addressed cross-modal predator recognition and the impact of sensory modes in which information about predator presence was perceived. Although habituation and dishabituation stimuli in both groups referred to buzzard presence, pigeons in group 3 were confronted with acoustic cues in the dishabituation phase, which we expected to encode lower levels of urgency (compared to previous information in the visual domain) whereas birds in group 4 were presented with visual models that we expected to represent an increased level of urgency (compared to acoustic playbacks during the habituation phase).

Every pair of pigeons was tested only once. The experiment for each pair included the baseline, the habituation and the dishabituation phases. At the beginning of each experiment all pigeons except the focal pair were removed from the test aviary and remained in visual and acoustic isolation throughout the experimental phase. Visual and acoustic stimuli were displayed at approximately the same distance (±0.5 m) to the focal aviary.

Table 1 Experimental conditions ("information" refers to the informational content of the dishabituation stimulus as compared to the habituation stimulus).

Group	Habituation	Dishabituation	Information
1	Pheasant visual	Buzzard visual	Predator presence, high urgency
2	Pheasant acoustic	Buzzard acoustic	Predator presence, low urgency
3	Buzzard visual	Buzzard acoustic	Decreased urgency
4	Buzzard acoustic	Buzzard visual	Increased urgency
5	Pheasant visual	Buzzard acoustic	Predator presence, low urgency
6	Pheasant acoustic	Buzzard visual	Predator presence, high urgency

Baseline

The empty cardboard box was placed in front of the open door of the aviary at a height of 60 cm and was present throughout the experiment over all groups. We displayed all models at this elevated level as most raptors perch on the ground only after capturing prey and thus no longer represent an urgent threat Hence, the elevated presentation of bird models was designed to control for realistic circumstances of risky predator presence. Additionally, this height was chosen to guarantee good visual access from the aviary. The sliding door was opened and closed constantly to habituate the birds to the equipment. As soon as the focal subjects no longer paid any attention to the procedure and returned to self- or partner-directed behaviour (e.g. preening, sleeping, feeding), their behaviour was recorded for 5 min.

Habituation

As we could not prevent adjacently housed pigeons from eavesdropping on displayed acoustic stimuli, we started with birds that were assigned to groups in which the habituation stimulus was a visual model. Hence, we avoided repeated exposure to acoustic stimuli for birds before they were actually tested. To avoid continuous exposure to visual models for birds except the focal pair, we positioned the cardboard box in such a way that only the focal pair had full visual access to the model presented inside. Between groups, we included a break of 2 weeks between acoustic habituations and a break of 1 week between visual habituations to avoid the simulation of predator presence at a frequency likely to exceed naturally occurring predator encounters.

For visual presentations, the stuffed model was positioned in the cardboard box and was repeatedly visible to the birds for 20 s to ensure that birds saw the stimulus. As birds were expected to engage mainly in self- or partner-directed behaviour (e.g. sleeping, feeding, preening), a presentation length of 20 s was chosen to guarantee that the pigeons perceived visual stimuli. Presentation phases were separated by 20 s during which the box was closed and the model occluded. These 40 s, consisting of one presentation and the break, were defined as a trial. Trials were repeated until the focal pair returned to baseline behaviour. We continued data collection for six more trials of which the last three were used to analyse the birds' habituated behaviour. For acoustic habituations, the birds were habituated to either territory calls of pheasants (about 3.4 s) or buzzards (about 5 s), followed by 20 s silence. The number of buzzard territory calls in a sequence that occurs naturally was chosen as a reference for stimulus lengths in the auditory domain to make predator presence as ecologically valid as possible. Hence, although presentation times were shorter for acoustic than for visual presentations, they are likely to resemble realistic conditions because pigeons are not expected to perceive acoustic and visual cues of real-life predators of exactly the same length. The cardboard box was also present during playbacks. The speaker amplifier was placed near the aviary but not in the bird's direct visual range (behind the cardboard box) to prevent the birds from identifying the source of acoustic stimuli. Again, we defined the duration of the habituation phase by the birds' return to baseline behaviour and carried out six more trials of which the last three were analysed for the comparison with behavioural responses to dishabituation stimuli.

Dishabituation

After the focal birds were habituated to the assigned stimulus, the dishabituation stimulus was displayed. The respective stimulus was presented once and the behavioural response of the pigeons was recorded until the birds returned to baseline behaviour. For visual dishabituation, the model was displayed for 20 s, as in the habituation phase. After presentation, the sliding door was closed and remained closed until the focal pair showed baseline behaviour again. For acoustic dishabituation, the calls of the buzzards were played for 5 s and the bird's behaviour was recorded until they returned to baseline behaviour.

Statistical analysis

To examine whether the referent of the stimulus or the sensory mode of presentation has had an effect on the number of trials the birds needed to habituate, a Kruskal–Wallis test was applied over all six groups. As the data did not meet the assumptions of normality (Kolmogorov–Smirnov test: P=0.687) or homogeneity of variance

(Levene's test: $P=0.013$), we used nonparametric Mann – Whitney *U* tests, including a Bonferroni correction ($\alpha<0.0125$) to compare the number of trials to habituation. To examine whether the birds' perceived habituation and dishabituation stimuli as providing different or equivalent information, we compared behavioural responses in both experimental phases. However, as the detailed nature of pigeons' antipredator response has not been described, we reduced all 17 encoded behavioural variables to independent components using a principal component analysis (PCA). Components with eigenvalues of at least 1 were extracted and a varimax-rotated correlation method was used. As some of the variables had high loadings on more than one component (>0.4), we had to eliminate eight of our originally measured variables, resulting in nine variables with simple structure (see Table A2 in the Appendix). To ensure consistency in video coding, 10 randomly chosen sample recordings were double coded by a second person who had no knowledge about the stimuli displayed in the videos (visual stimuli were not visible in recordings and videos were presented without sound). The interobserver reliability tests revealed high Cohen's kappa (κ) coefficients for all nine variables (all $\kappa\geq0.88$, see Table A3 in the Appendix for details). The comparisons of the number of trials to habituation and the PCA were conducted using SPSS v. 17.0.1 (SPSS Inc., Chicago, IL, U.S.A.).

Afterwards, the condensed variables were entered in within-group comparisons between the habituation and the dishabituation phases using Wilcoxon signed-ranks tests. One-tailed P values were calculated in accordance with clearly directed predictions. Owing to small sample sizes per group ($N=5$) and inaccurate calculations of *P* values in most common statistical packages (in which the test statistic is anticipated to approach a normal distribution asymptotically, independently of sample size), we calculated the test statistic (*T*) by hand and obtained one-tailed *P* values (Mundry & Fischer, 1998).

RESULTS

Trials to habituation

There were significant stimulus-dependent differences in the number of trials that the birds needed to habituate to presentations (Kruskal–Wallis test: $\chi^2_3=13.76$, $P=0.003$). Pigeons needed significantly more trials to habituate to simulated buzzard presence than to pheasant displays in the acoustic domain (Mann–Whitney *U* test: $U=3.5$, $N_{\text{buzzard}}=5$, $N_{\text{pheasant}}=10$, $P=0.005$). The birds also needed more trials to habituate to buzzard models than to pheasant models, although this effect was not significant after Bonferroni corrections (Mann–Whitney *U* test: $U=8$, $N_{\text{buzzard}}=5$, $N_{\text{pheasant}}=10$, $P=0.03$). The effect of the sensory mode of stimulus presentation was significant for pheasant (Mann–Whitney *U* test: $U= 12.5$, $N_{\text{visual}}=N_{\text{auditory}}=10$, $P=0.003$; Fig. 2) but not for buzzard displays (Mann–Whitney *U* test: $U=9$, $N_{\text{visual}}=N_{\text{auditory}}=5$, $P=0.548$). The presentation of buzzard models also resulted in longer habituation phases than pheasant calls (Mann–Whitney *U* test: $U=3.5$, $N_{\text{buzzard\_visual}}=5$, $N_{\text{pheasant\_auditory}}=10$, $P=0.005$). Pigeons did not need more trials to habituate to buzzard calls than to pheasant models (Mann–Whitney *U* test: $U=22$, $N_{\text{pheasant\_visual}}=10$, $N_{\text{buzzard\_auditory}}=5$, $P=0.768$; Fig. 2). Hence, although simulated predator presence in general elicited stronger responses than control displays, the sensory mode of perception also affected the pigeons' behavioural response.

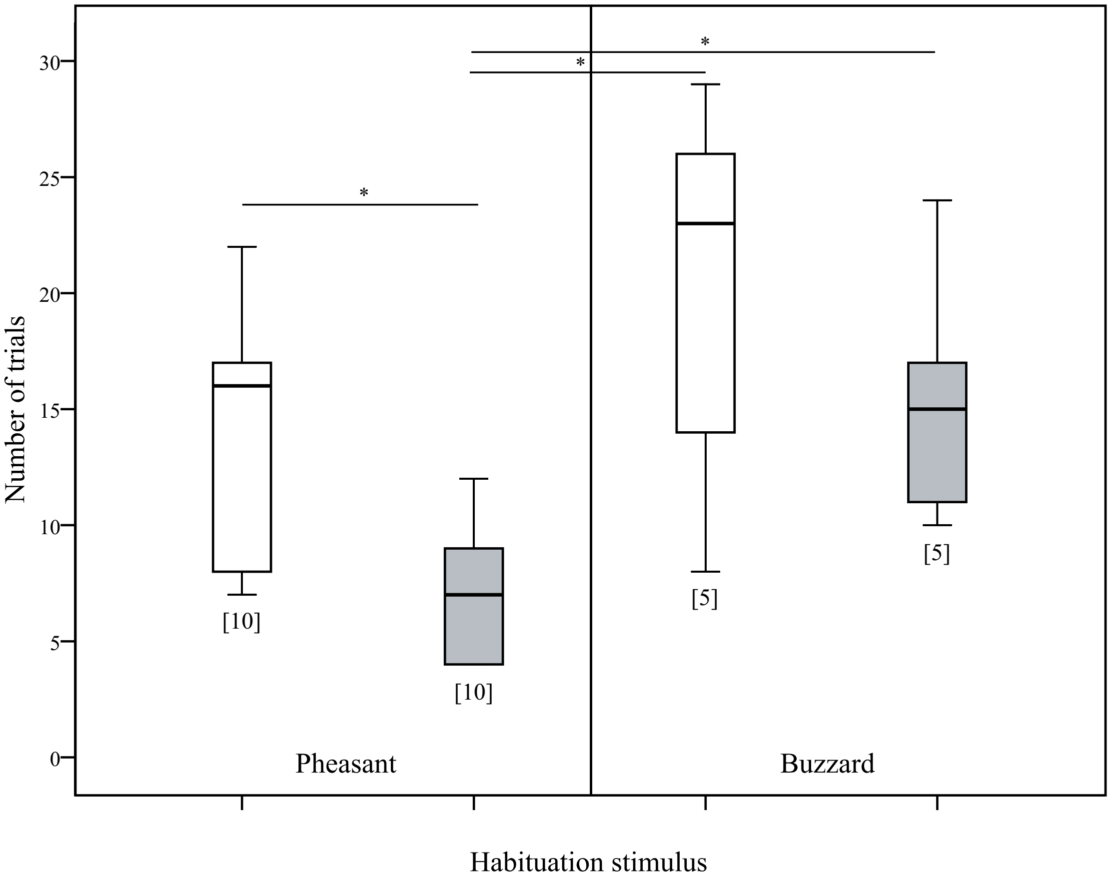

Figure 2 Number of trials the pigeons needed to habituate to pheasant (left) and buzzard (right) stimuli. Boxplots in grey indicate acoustic playbacks; boxplots in white refer to visual models. Numbers in brackets represent the number of dyads that were habituated with each stimulus and "*" indicate statistical significance after Bonferroni corrections (*P*<0.0125). The bottom of each the box indicates the first; the top indicates the third quartile. The horizontal line within each box represents the median. Whiskers include values that amount to 1.5 times the height of the box (interquartile range).

Behavioural response

A PCA revealed four independent components in the pigeons' overall response that accounted for 78% of the total variance. The calculated components corresponded to general contexts of behaviour (Table 2). Three of them were observed during normal, daily activity patterns of the birds. Sleeping behaviour was clustered together with retracting the neck and fluffing up the plumage and corresponded to 'resting behaviour'. Approaching and feeding the partner were also positively correlated and together comprised 'partner-directed behaviour'. Looking at the stimulus and neck stretching together with scanning represented general attentive behaviour, summarized as 'vigilance'. The fourth, independent component was exclusively observed in the context of simulated predator presence. The birds responded only to visual buzzard displays and buzzard calls with rapid 'scanning back and forth in the horizontal plane' ('nystagmus'), a behaviour that was formerly reported as part of antipredator responses in chicken (Evans, 2002). This predator-specific behaviour was performed together with scanning behaviour and was directed to the stimulus or up into the sky.

Table 2 Independent variables revealed from Principal Component Analysis.

	PC 1	PC 2	PC 3	PC 4
context	resting behaviour	partner directed behaviour	vigilance	predatory response
variance explained (%)	28.8	23.1	14	11
variables	retracting neck fluffing up sleeping	approaching partner feeding	looking to stimulus stretching neck and scanning	looking to stimulus+nystagmus looking above+nysstagmus

Effect of stimulus order and sensory mode

To investigate whether pigeons interpreted dishabituation stimuli as transmitting different information to habituation stimuli, we compared principal components of behavioural responses in both phases by means of Wilcoxon signed-ranks tests. Predator-specific scanning behaviour (component 4) was reliably shown whenever buzzard representations followed pheasant displays, independent of the physical properties of the signal (comparison within groups 1, 2, 5, 6; Wilcoxon signed-ranks tests: each T=0, N=5, P<0.05). Pigeons also responded with an increase in predator-specific scanning to buzzard models that followed buzzard calls (Wilcoxon signed-ranks tests: group 4: T=0, N=5, P<0.05; Fig. 3). In contrast, the birds showed neither increased levels of attentiveness (component 3) nor predator-specific scanning when the order of stimulus presentation was switched and buzzard playbacks followed visual presentations of the buzzard. In addition to predator-specific scanning behaviour pigeons showed an increase in general attentiveness to models of the buzzard following pheasant visual presentations (Wilcoxon signed-rank tests: group 1: T=0, N=5, P<0.05) or pheasant calls (Wilcoxon signed-rank tests: group 6: T=0, N=5, P<0.05). The birds did not show any increase in vigilance to buzzard calls following pheasant displays or visual presentations of the buzzard following buzzard calls (Fig. 3). In summary, the effectiveness of information about buzzard presence in eliciting antipredator behaviour depended on the pigeons' past and current experience. We did not find any differences in 'resting' (component 1) or 'partner-directed behaviour' (component 2) between experimental phases in any of the groups.

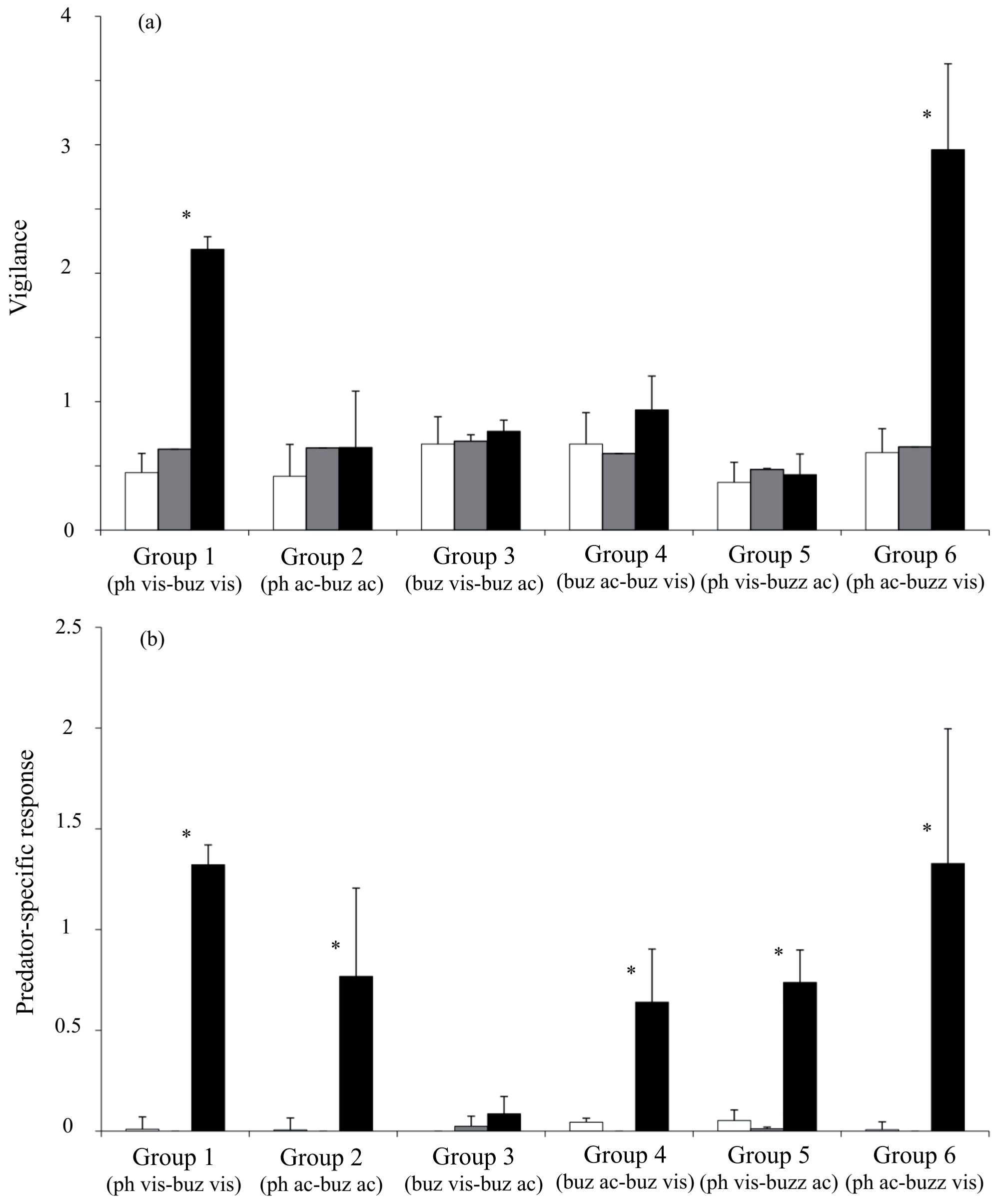

Figure 3 Estimated vigilant (a) and predator-specific (b) response at the end of baseline (white bars), at the end of the habituation (grey bars) and during the dishabituation phase (black bars). Abbreviations below group numbers indicate the stimuli presented during the habituation and the dishabituation phase (ph vis=pheasant model; ph ac=pheasant calls; buz vis=buzzard model; buz ac=buzzard calls). Asterisks indicate significant differences between behavioural responses in the habituation and the dishabituation (one-tailed *P*- values <0.05) and were obtained by calculating Wilcoxon signed rank tests by hand and comparing the test statistic (*T*) with critical values from tables.

DISCUSSION

The present results provide the first evidence that individuals of a species that does not produce specific alarm calls take past information about predator presence cross-modally into account and adjust their behaviour accordingly. Critically, the pigeons' responses cannot be explained on the basis of mere associative learning in terms of the same physical signal properties reliably eliciting the same behavioural response. Several species have been shown to integrate cross-modal representations of conspecifics (Proops et al., 2009; Sliwa et al., 2011) and heterospecifics (Adachi et al., 2007). However, these advanced capabilities do not prove these species have the tremendous flexibility in information processing that is essential to react selectively to the same information, depending on the context in which it is perceived. Nonhuman primates (e.g. Zuberbühler, 2000; Seyfarth & Cheney, 2008) and birds (e.g. Evans, 2002) that produce alarm calls are known for the ability to infer the value of information by comparing it with previous knowledge. Our results suggest that the cognitive mechanisms underlying this ability are also present in a bird species that does not produce such vocalizations, which supports the idea that interpretative mechanisms are part of the more general ability of abstract class formation. The birds showed specific predator-related behaviour only to buzzard stimuli in cases in which they were newly informed about predator presence or the threat was considerably more urgent. The birds did not show any response to buzzard calls when they were previously warned of its presence by visual presentations of the buzzard. In contrast, pigeons consistently showed predator-specific behaviour, but no general attentive behaviour, whenever buzzard models followed buzzard calls. We suggest that although the referent of the signal was the same (buzzard), the inferred information also depended on the order of stimulus presentation and additional information was coded by the modality of signals. Thus, the pigeons' behavioural response regarding general attentiveness and predator-specific scanning behaviour to displayed stimuli was based on the reference of the signal, the novelty of the information and the perceived urgency rather than on the signals' physical properties alone.

Raptors are frequently present in the pigeon's environment and produce calls without actually attacking. The birds thus benefit from a reliable perception of the raptors' presence but they should not always react as they do during predation events (Warkentin et al., 2001). However, if pigeons visually perceive the potential threat in their vicinity (as simulated during visual presentations), the risk of predator attacks, and thus the level of urgency, is increased. The importance of visual information for the inference of urgency and predation avoidance is further supported by the fact that the stuffed models of the pheasant and the buzzard required a similar number of trials for the birds to habituate to them. As the pheasant model was similar in size and plumage colour to the buzzard model, the pigeons might have perceived pheasant models as unfamiliar, disturbingly close and considerably big birds, although they were not interpreted as being as threatening as the buzzard model. The pigeons did not show any general attention (indicated by scanning and general vigilance) to visual stimuli after acoustic habituation to the buzzard, as if they had already inferred the presence of the buzzard by its calls, but instantly looked at the stimulus (when the box was open) and above (after the box was closed) and performed characteristic scanning behaviour. This predator-specific scanning behaviour manifests in rapid back and forth head movements that facilitate fast depth perception by motion parallax. Especially for birds of prey with laterally placed eyes and little binocular overlap, motion parallax is thought to function to estimate predator distance reliably (Evans, 2002). As the position of stimulus presentation was kept constant in both sensory modes, we consider it unlikely that any variables (e.g. distance to playback source/models) other than the sensory mode encoded different levels of urgency in our study. However, a possible alternative interpretation of the present results may be considered. As pigeons reacted with predator-specific scanning behaviour also to visual presentations of the buzzard that followed buzzards' calls, it may be argued that birds did not integrate predator cues cross-modally but only showed reliable discrimination of predator (buzzard) and nonpredator (pheasant) within one sensory mode and that they generally perceive visual displays as being more urgent. However, we consider this explanation highly unlikely for two reasons. First, the pigeons' behavioural responses were composed of two independent components (vigilance and predator-specific scanning). If we take both independent variables into account, the birds did not show the same responses whenever visual buzzards were presented. Although they responded with predator-specific scanning behaviour to buzzard models after they were habituated to buzzard calls (probably to gain more information about the exact distance of the threat), we did not find increased levels of general vigilance. In contrast, when visual buzzard presentations followed pheasant stimuli, pigeons were significantly more vigilant, engaged in scanning the surroundings and additionally performed predator-specific scanning during dishabituation. Second, the pigeons needed comparable numbers of trials to habituate to buzzard calls and to the buzzard model, suggesting that these stimuli were perceived as being equally disturbing. What we cannot (and do not) claim is to have identified the level of discrimination. Our results show that pigeons recognized predatory and nonpredatory stimuli. The exact referent of the applied functional concept, namely whether pigeons actually recalled mental representations of buzzards in particular, aerial predators or a predator in general has to be addressed in further studies.

Taken together, the present study suggests that advanced mechanisms of contextual interpretation of external information in the context of predation can also be found in species that do use specific signals such as alarm calls. This extends the cognitive abilities found in nonalarm-calling species and supports the previously found disparity in cognitive abilities of signallers and receivers in highly vocal species.

Pigeons have been shown to apply highly sophisticated concepts such as familiarity (Nakamura et al., 2003), people–nonpeople (Herrnstein & Loveland, 1964; Aust & Huber, 2006), heterospecific discrimination (Belguermi et al., 2011) and representational transfer between objects and their pictures (Aust & Huber, 2010) in visual discrimination tasks but, to our knowledge, have not been shown to possess cross-modal contextual understanding in a predatory context. Pigeons may discriminate on the basis of functional classes between predators and nonpredators, or recognize different subcategories (e.g. aerial and ground predators) or even species of predators. To tackle the level of classification, different species of predators and nonpredators could be used and the pigeons' cross-modal transfer between these could be tested. If pigeons reacted differently to both predators, depending on the stimulus species and not on the general context of predation, one could successively exclude crucial features of recognition. However, if pigeons discriminate on the basis of 'predators' and 'nonpredators' we would expect the same results as presented here. To test different cognitive mechanisms that underpin communicative abilities in sending and receiving signals, further studies on nonalarm-calling species may investigate their abilities regarding, for example, heterospecific alarm call recognition, audience effects or predator specificity of behavioural responses.

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SUPPLEMENTARY MATERIAL

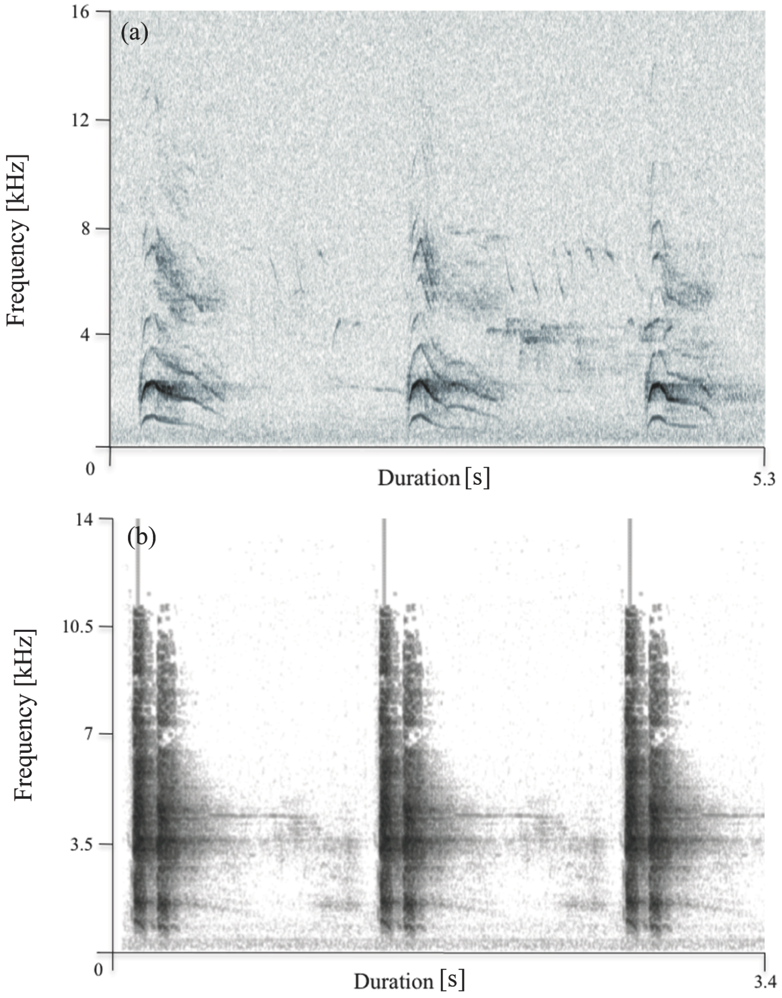

Figure A1 Spectrograms of acoustic stimuli. (a) buzzard territory calls, (b) pheasant territory calls.

Table A1 Response variables. Descriptions of original variables are given and principle components on which the variables loaded are indicated as well as which variables had to be excluded due to their complex structure (loadings >0.4 on more than one component).

	Variable	**Description**
PC 1 (“resting”)	Retracting neck	Retraction of neck, individual sitting or standing on perch, plumage splayed out
	Fluffing up	Plumage splayed out, individual sitting or standing on perch
	Sleeping	Individual sitting, beak in plumage at the back, eyes closed
PC 2 (“partner directed”)	Approaching partner	Direct approach to conspecific, resulting in high spatial proximity (usually directly next to each other)
	Feeding	Pigeon puts its beak into the partner’s bill
PC 3 (“vigilance”)	Looking to stimulus	Looking to cardboard box (in combination with neck stretching)
	Stretching neck & scanning	Stretching the neck in combination with scanning behaviour
PC 4 (“predatory response”)	Looking to stimulus + predator related scanning behaviour (nystagmus)	Looking to cardboard box + rapid, high frequent back and forth neck movement of the neck (in one direction, due to motion parallax)
	Looking above + predator related scanning behaviour (nystagmus)	Looking above + rapid, high frequent back and forth neck movement of the neck (in one direction, due to motion parallax)
Variables with complex structure (removed)	Looking above	Looking above (not coded if the pigeon flies to a perch above afterwards)
	Looking to partner	Looking to conspecific; not coded during partner directed behaviour (e.g. feeding)
	Foraging	Looking for and pecking food with head bowed
	Grooming	Allo-grooming
	Preening	Self-preening, cleaning the plumage with the beak or scratching with the claws
	Approaching stimulus	Pigeon situated on the floor and moving towards the cardboard box while looking at it
	Retreat from stimulus	Quick retreat from box
	Stretching	Stretching of wings and legs

Table A2 Interobserver reliability. Cohen’s kappa coefficients are given for single variables.

Behavioural variable	κ
Retracting neck	0.97
Fluffing up	0.97
Sleeping	0.95
Approaching partner	0.92
Feeding	0.88
Looking to stimulus	0.99
Stretching neck & scanning	0.92
Looking to stimulus + nystagmus	0.98
Looking above + nystagmus	0.97

Table A3 Rotated component matrix. Loadings of original variables on the different components are presented. Loading higher than 0.4 are highlighted in bold.

	Component			
	1	2	3	4
Retracting neck	**0.74**	-0.244	-0.087	0.014
Fluffing up	**0.857**	-0.17	-0.175	0.29
Sleeping	**0.852**	0.057	0.151	-0.087
Approaching partner	-0.156	**0.869**	-0.025	0.171
Feeding	-0.92	**0.872**	-0.08	0
Looking to stimulus	0.064	-0.321	**0.814**	-0.107
Stretching neck & scanning	-0.109	0.129	**0.81**	0.019
Looking to stimulus + nystagmus	0.17	-0.021	0.147	**0.871**
Looking above + nystagmus	-0.08	0.258	-0.326	**0.784**

CHAPTER 3: PIGEONS DISCRIMINATE OBJECTS ON THE BASIS OF ABSTRACT FAMILIARITY

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accepted in

Animal Cognition

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ABSTRACT

Knowledge of previous encounters with conspecifics is thought to be beneficial as it allows fast and appropriate behavioral responses towards those animals. This level of categorization goes beyond perceptual similarity and requires the individual to refer to a more abstract common referent, namely familiarity. It has been shown that pigeons are able to form functional classes of conspecifics that are based on familiarity. To date, we do not know whether this ability is restricted to the social context (including heterospecifics) or if it can also be used to classify inanimate objects. Furthermore, the factors influencing the formation of this functional class are still unknown. Here we show that pigeons (*Columba livia*) are able to use a categorical rule of familiarity to classify previously unseen photographs of objects from their living environment. Pigeons that lacked real-life experience with the objects were not able to do so. This suggests that perceptual features alone were not sufficient for class recognition. To investigate the impact of additional functional properties of the objects, familiar objects were further divided into two subcategories, namely those that were considered functionally relevant to the birds and those that were not. Although the majority of pigeons learned to categorize photographs of objects based on familiarity alone, our results also suggest an unlearned preference for "relevant" familiar objects. The results presented here suggest that pigeons are able to learn to extract the discriminative feature of abstract familiarity from pictures by referring to previous real-life experience but that additional functions of objects lead to a preference of these objects.

Keywords: familiarity, pigeon, inanimate objects, functional relevance, picture-object recognition, abstract categorization

INTRODUCTION

Categorization is one of the most fundamental cognitive processes as it allows an individual to efficiently reduce the vast amount of information that it perceives and takes advantage of the fact that objects within the same category share many properties. Animals may categorize stimuli in several different ways (for recent reviews, see Zentall et al., 2008; Huber, 2010). One mechanism with which individuals could sort objects is to use perceptual features. Stimuli that share perceptual features are likely to belong in the same class. However, in nature, these classes are likely to be based on more abstract object properties, such as ‘food,’ ‘tool,’ or ‘enemy’. As these categories are based on the function of the stimuli, they are referred to as a “functional classes”. This goes beyond categorization on the basis of perceptual features and allows correct classification of exemplars that bear no physical similarity to each other (Lea, 1984; Huber, 2010). Categorization on the basis of familiarity is one such example. By this, individuals are required to refer to individual pre-experience with class members, namely previous encounters, for successful categorization.

Most previous research on familiarity-based recognition has focused on conspecific recognition (e.g. Van Dyk & Evans, 2007; Wilkinson et al., 2010; Tricario et al., 2011) or heterospecific recognition (e.g. Stephan et al., 2012; Wascher et al., 2012). Heterospecific recognition is considered particularly beneficial for predator avoidance (Slobodchikoff et al., 1991; Levey et al., 2009) and in captive situations (Taylor & Davis, 1998; Racca et al., 2010; Stephan et al., 2012). Hence, familiarity is thought to serve as a useful discriminative feature whenever different individuals could be classified according to a common function or consequence. Despite the importance of this discriminative feature, the nature of the underlying learning mechanisms is still not fully understood. Is the formation of functional classes based on familiarity restricted to the receiver's broader social life (Whiten & Byrne, 1997; Tibbetts & Dale, 2007)? To date, we do not know whether perceivers also recognize inanimate objects in their everyday life on the basis of previous encounters.

Taking the theoretical requirements of functional classes into account, it seems reasonable to investigate recognition on the basis of familiarity for all external entities that have the potential to be relevant to the receiver by either the inherent function they provide or by eliciting an appropriate behavioral response. Systematic experiments on the discrimination of familiar and novel inanimate objects that cannot be classified by only perceptual cues are still scarce and have often revealed inconsistent results (Kendrick, 1992; Wilkie et al., 1992; Dawkins et al., 1996 on the discrimination of familiar landscapes). Convincing support for the notion that pigeons are sensitive to previously shown inanimate stimuli comes from a study that used pictures of complex objects (Macphail & Reilly, 1989), which were either "familiar" (pictures previously seen by pigeons) or "novel" (never seen before). However, this study mainly referred to the short-term memory of pigeons for perceptually complex pictorial stimuli and did not investigate pigeons' ability to infer "familiarity" that was based on previous real-life experience with objects that were presented as photographs.

Pigeons are known for their advanced abilities in visual discrimination tasks (e.g. Huber, 2000; Huber et al., 2000; Aust & Huber, 2002; Huber & Aust, 2011) and there is recent evidence that they can also classify conspecifics on the basis of familiarity (Wilkinson et al., 2010). Wilkinson et al. (2010) showed that although recognizing real life entities in 2D-representations is not at all simple (e.g. Delius et al., 2000; De Loache, 2000), pictorial representations of conspecifics alone were sufficient for birds to classify them on the basis of familiarity. This further supports the idea that pigeons are able to infer the correspondence between pictures and their real-life referents (Aust & Huber, 2006, 2010) and is consistent with other studies that successfully confronted mammals with 2D-images of conspecifics and heterospecifics (Kendrick et al., 1996; Coulon et al., 2009).

Given the pigeons' ability to classify on the basis of familiarity in a social context, they are the ideal subjects to examine similar processes using inanimate objects. Thus, the present study investigated whether pigeons could classify pictures of inanimate objects from their everyday life on the basis of familiarity. We trained pigeons to discriminate between 2D-representations of familiar objects and objects that they had never encountered before. Afterwards, we presented the birds with different instances of familiar objects that they had real-life experience with but which they had never seen during training and novel unfamiliar objects. Identical stimuli were also presented to a control group of birds that did not have real-life experience with any of the objects. We predicted that the experimental birds would be able to classify instances of familiar objects that had not been previously shown as pictures whereas control birds would master a generalization test but fail in the critical classification test with pictures of familiar objects that had not been previously shown as photographs. In addition, we included some familiar objects that we considered to have an additional ecological function for the birds in the aviaries. By doing this we aimed to investigate the potential impact that different levels of relevance might have on learning and recognition of stimuli. If relevance indeed influences the choice behavior of birds, we expect experimental but not control birds to show a preference for these.

MATERIALS AND METHODS

Subjects

We used 16 pigeons and allocated them to two groups based on their opportunity to gain real-life experience with some of the objects (that were later shown as photographs) before the discrimination training. Nine homing pigeons were assigned to the experimental group (object experience) and 7 homing pigeons to the control group (object naïve). All birds of the experimental group lived together in an outdoor aviary (2.9m x 2m and 3m high). The control birds shared an aviary (2m x 1m and 2m high) and had no visual contact with any of the objects. All aviaries were equipped with perches, nesting boxes and a water dispenser. Water and grit were freely available throughout the entire experiment. Food was provided during experimental sessions, at the end of the day and over the weekend. All birds were maintained at a minimum of 90% of their free feeding weight.

Stimuli

Real Objects

We introduced 16 previously unseen objects to the experimental birds. All objects were introduced 14 days before the first training session and remained in the birds' surroundings throughout the experiment. Of these objects, eight were considered functionally relevant to the birds and eight were not. Functional relevance referred to object properties that were thought to provide any function to the birds or triggered the birds' attention and interest, which might also lead to more time that the birds spent either interacting or observing these objects (food trough, water dispenser, perch, nesting box, a tray that provided food, grit bowl, basket for nesting opportunities and a modified ledge for perching). Functional irrelevance was assigned to objects without any expected function (green watering can, protective helmet, hanging bottle, broom, cup, small figure, pencil box and sponge). Importantly, all these objects were chosen to provide a minimum of perceptual similarity. The experimental birds had the opportunity to become familiar with these introduced objects. Unfamiliar objects were photographed and shown as pictorial stimuli only. This means that pigeons did not encounter any of these objects in real life. We chose these objects according to their visual similarity with familiar objects (e.g. shape, color), to ensure that the pigeons did not solve the task using simple perceptual features (see Online Resource 1 for pictures of all objects). The experimental group was visually naïve to all unfamiliar objects and the control group had never seen any of the objects (and was thus unfamiliar to all object stimuli).

Photographic Stimuli

The pigeons were presented with color photographs of objects that were familiar to the experimental group from their aviary experience (familiar objects) and objects that were completely unknown to both groups of pigeons (unfamiliar objects). Although none of the objects was previously seen by control birds (and all pictorial presentations were unfamiliar to them), we will refer to "familiar" and "unfamiliar" sets of pictures to both groups to indicate the impact that previous experience had on the performance of experimental birds. All objects were photographed from 14 different angles with a Pentax K10D digital camera. Within all sets of photographs, we controlled for color, shape and size. When displayed on the touch-screen monitor each stimulus measured 3.8 x 3.8 cm (449 x 449 pixel). To prevent discrimination due to any salient background feature, all photographs were manipulated to have the same beige background using Photoshop software (© Adobe Inc.). This color was chosen to provide a high level of contrast with all stimulus objects (for examples of photographic stimuli please see Online Resource 1).

Apparatus

The birds were trained and tested in an indoor Skinner box measuring 50 x 30 x 40 cm. At one end of the box, an infrared touch frame was installed in front of a 15 inch (38 cm, diagonal) PC monitor (Panasonic PanaSync 4G). Food was provided directly in front of the monitor via a feeder system that comprised a motor unit and piston. The latter was lifted and illuminated after each correct training choice (Steurer et al., 2012). All experiments were controlled by the "CognitionLab" software package (developed by M. Steurer).

Procedure

The birds were trained using a two-alternative forced choice procedure. Two photographs were presented next to each other on a touch screen monitor. Pecking on the positive stimulus resulted in "positive" acoustic feedback (600Hz frequency) and a 3-sec feeding period. Pecking on the negative stimulus led to "negative" acoustic feedback (200Hz frequency), the monitor turning red (3 sec) and a correction trial (repetition of last trial in a loop until the positive stimulus was chosen). There was no differential feedback during test trials. The minimum number of pecks that was required to indicate choice performance was set to one. Hence, the stimulus at which the subjects pecked first in each trial entered the analysis. Each trial was followed by an inter-trial interval of 6 sec during which time the monitor was dark. The left-right position of familiar and unfamiliar objects was randomly assigned for each trial. All views of familiar and unfamiliar photographs were paired randomly and contingencies of rewarded stimulus type were counterbalanced across subjects. Thus, four pigeons of the experimental group were rewarded for choosing the familiar photographs whereas five were rewarded for choosing unfamiliar stimuli (control group: four for familiar positive, three for unfamiliar positive). To ensure that the experimental pigeons were not making the discrimination using any spurious perceptual features in the photographs, each pigeon in the experimental group received stimuli that were exactly matched with an animal in the control group (two of the experimental birds, each had stimuli that were matched with two control birds). Additionally, we assigned different objects as training- and test stimuli to each of these pairs of pigeons. The subjects received one to two training or test sessions a day, five days a week.

Discrimination training

Photographs of 10 familiar and 10 unfamiliar objects (of the familiar objects 5 were considered functionally relevant and 5 were considered irrelevant) were used for training; each object was presented at 10 different viewing angles. Each training session comprised 50 trials. Criterion of mastery was met when the pigeon had completed at least 25 sessions and made correct first choices in 80% of the trials (40 correct first choices out of 50 trials) in four out of five consecutive sessions and at least 75% (38/50) in the remaining session. If a subject did not reach criterion after 75 sessions, training ceased and the bird was excluded from the rest of the experiment.

Generalisation test

All birds that successfully mastered the training task were given a Generalization test in which they were presented with four novel views of the training stimuli (both familiar and unfamiliar). The Generalization test was used to test whether pigeons of both groups were able to generalize to novel views of training stimuli, using perceptual features alone. Each session comprised 50 training trials and 10 test trials. This resulted in a total of 60 trials in each test session. Each test trial showed unseen views of a familiar training object paired with an unseen view of an unfamiliar training object. Thus, 40 completely novel views of familiar and unfamiliar objects were presented in the test. Each of the test photographs was presented twice (only once in a session and paired in novel combination for each presentation), resulting in 80 test trials presented over 8 sessions.

Object familiarity test

After the birds had successfully completed the Generalization test they entered the Object familiarity test. This second, critical, test was conducted to examine whether the experimental pigeons were able to classify instances of familiar objects from their aviary that have not been seen as pictorial presentations before using previous real-life experience as a discriminative feature. Further, it examined whether the supposed relevance of some of the familiar real objects had an effect on this discrimination. For this purpose, 50 training trials were intermixed with 12 test trials in each session. Test trials contained photographs of six objects that were familiar to the experimental group from their aviary experience but had never previously been shown as pictorial stimuli (randomly paired with six previously unseen unfamiliar objects). Again, 14 views were used for each object, resulting in 84 test trials that were distributed over 7 sessions. Of the six familiar objects that had not previously been seen during training, three were considered “functionally relevant” to the pigeons and three “functionally irrelevant”. All test photographs of familiar and unfamiliar objects were shown only once.

Data analysis

All comparisons were based on the number of correct choices of stimuli except for the analysis of the impact of relevance where we also included incorrect choices. To examine the differences in acquisition between the experimental and control birds, the number of sessions to reach training criterion for each group were compared using a univariate General Linear Model (GLM) with the number of sessions as the dependent variable and two independent variables, namely “group” (experimental or control) and “contingency” (rewarded for unfamiliar or familiar objects). As our predictions were clearly directed, a one-tailed binomial test was employed to assess training and test performances on an individual level. To be consistent over both groups, we also provide more rigid, one-tailed results for the control group, although predictions for the performance of control birds might be non-directional as well (random choice behavior). We used a meta-analysis to calculate chi-squared values from each individual p-value, derived from the binomial tests to pool individual performances. By this, we were able to control for sampling variation due to multiple individual tests and to assess the test performance in the experimental and in the control group (comparing correct and incorrect choices). Furthermore, we calculated performances of birds that were rewarded for choosing familiar and those that were rewarded for choosing unfamiliar objects separately within each group to distinguish between a learned and an unlearned preference for familiarity. Differences in the test performance of the two groups were calculated by comparing correct choices of both groups by means of one-tailed Mann-Whitney U tests. To evaluate the impact of the “relevance” of familiar objects we conducted individual one-tailed binomial tests for all birds that were rewarded for choosing familiar objects (in the experimental and the control group). We compared the proportion of relevant and irrelevant objects in correct choices to see whether experimental birds or control birds had a significant preference for objects that only experimental birds experienced to be functional in their everyday lives. For birds that were rewarded for choosing unfamiliar objects, we compared the proportion of relevant and irrelevant familiar objects in the errors they made during the object familiarity test (as correct choices in these birds referred to unfamiliar objects that were not experienced as being relevant or irrelevant previously).

RESULTS

Discrimination training

There was a tendency towards a greater number of sessions required to reach criterion in the control group (median: 38, range: 25-70) than in the experimental group (median: 28, range: 26-42). However, this difference was not significant ($F_{1,11} = 2.17$, P=0.169). There was also no effect of contingencies on sessions to criterion ($F_{1,11} = 0.165$, P=0.692) and no impact of the interaction group-contingency ($F_{1,11} = 0.01$, P=0.921).

Generalization test

All birds that reached discrimination criterion (8 experimental vs. 7 control pigeons) successfully transferred to novel views of the trained objects (binominal tests, all *P*-values≤0.001; Fig.1).

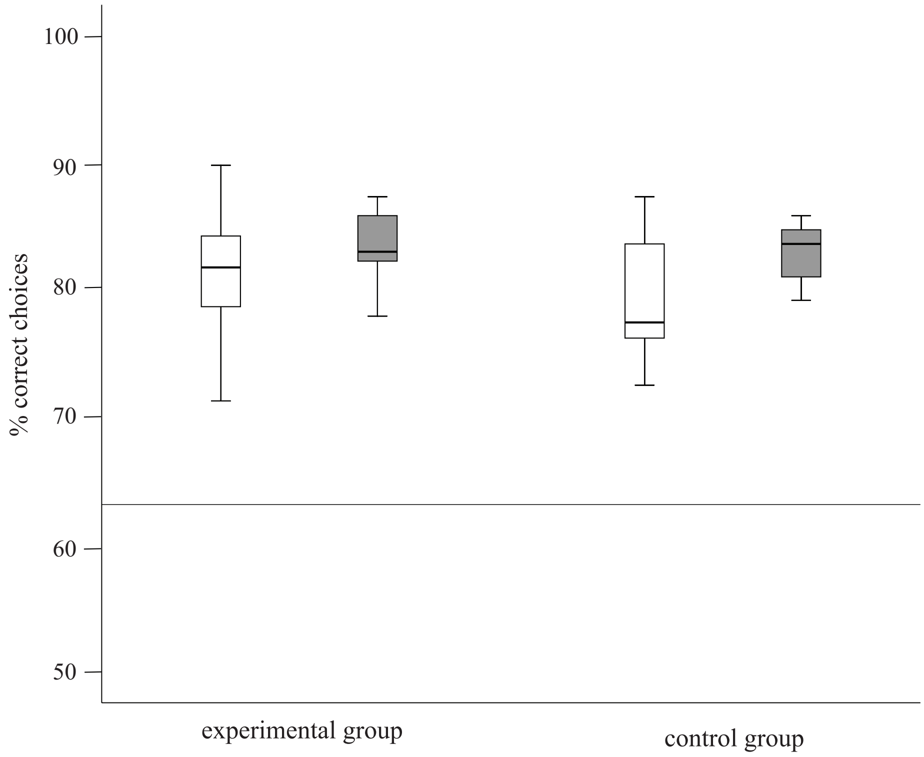

Figure 1 Performance in the Generalization Test. Percentages of correct first choices for experimental group and control group. White bars refer to the percentage of correct choices in test trials; dark bars represent the percentage of correct choices in intermixed training trials. The solid horizontal line indicates the level of significant discrimination.

Object familiarity test

Discrimination on the basis of familiarity

Six out of eight experimental pigeons transferred their discrimination to familiar and unfamiliar objects that have not previously been shown as pictures (binominal tests, all *P*-values ≤ 0.05, Fig. 2). Critically, all control birds failed in this test and could not distinguish between the stimuli on the basis of familiarity. Of the six experimental birds that passed this test, two were rewarded for choosing the familiar stimuli and four were rewarded for choosing the unfamiliar stimuli. On a group level, the experimental group significantly discriminated familiar and unfamiliar objects

(χ^2_{16}=61.92, $P \leq 0.0001$). To show that discrimination of objects was due to a learned concept of familiarity rather than to an unlearned preference for familiarity, we also analyzed the performance of subgroups, defined by the birds' contingencies. Both subgroups, consisting of S+ unfamiliar birds and S+ familiar birds, showed significant discrimination of test objects (subgroup$_{\text{unfamiliar}}$: χ^2_{10}=61.92, P=0.001; subgroup$_{\text{familiar}}$: χ^2_{6}=33.26, $P \leq 0.0001$). The control group failed to classify familiar and unfamiliar objects (χ^2_{14}=14.44, P=0.417). Comparing the number of correct choices in test trials, birds in the experimental group performed significantly better than those in the control group (Mann-Whitney U-test, one – tailed, $N_{\text{experimental}}$=8, N_{control}=7, U=7, P=0.007).

The impact of object relevance on choice behaviour

Experimental birds that were rewarded for familiar objects showed a significant preference for relevant objects (Table 1). Although one of the three S+ familiar birds did not master the object familiarity test, this individual also showed a significantly higher number of correct choices for relevant objects (individual: Bobby Tom, P=0.023). Interestingly, none of the control birds that were rewarded for familiar objects preferentially chose the functionally relevant objects (Fig. 3). Four of the five experimental birds that were rewarded for choosing unfamiliar objects made significantly more errors on relevant familiar objects than on irrelevant familiar objects. No such effect was found for the corresponding control birds (Table 1).

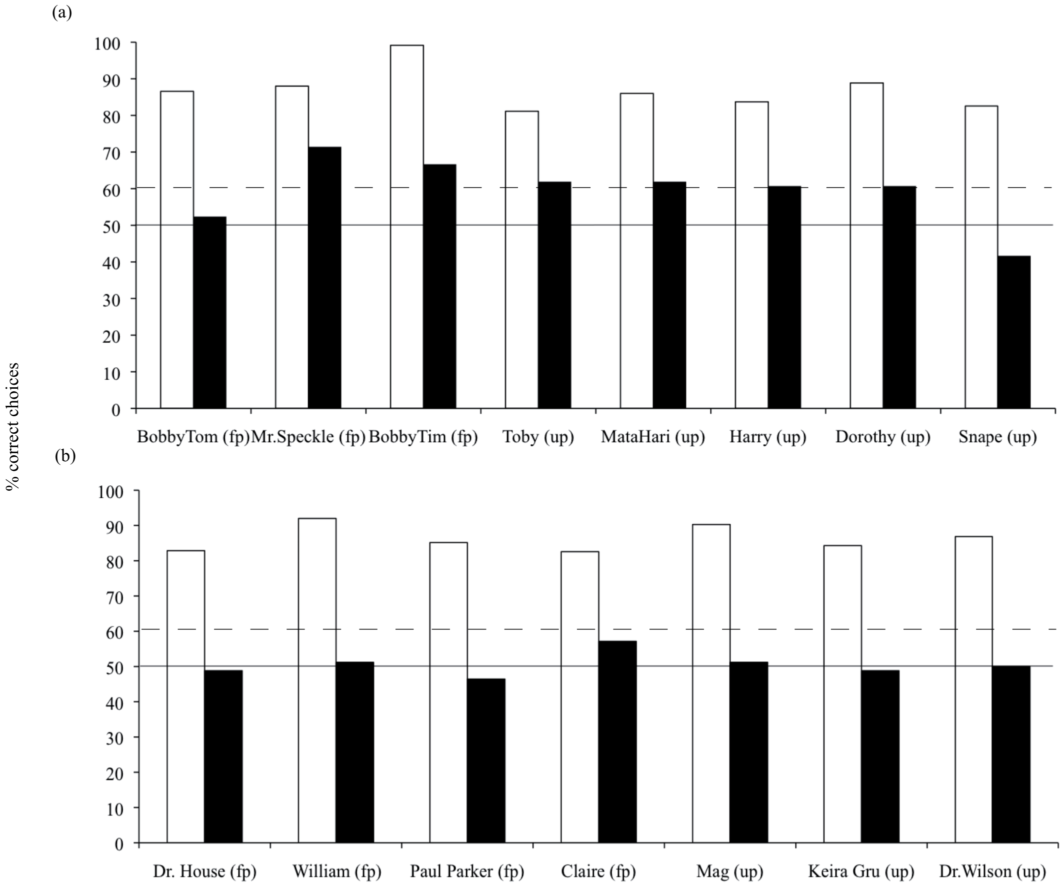

Figure 2 Performance in the Object-Familiarity Test. Percentages of correct first choices for (a) experimental group and (b) control group. White bars represent performance in training trials, black bars show performance in test trials. The solid horizontal line indicates chance level of performance, the dashed line indicates the level of significance. Abbreviations behind subject names: (fp) = contingency familiar positive, (up) = contingency unfamiliar positive.

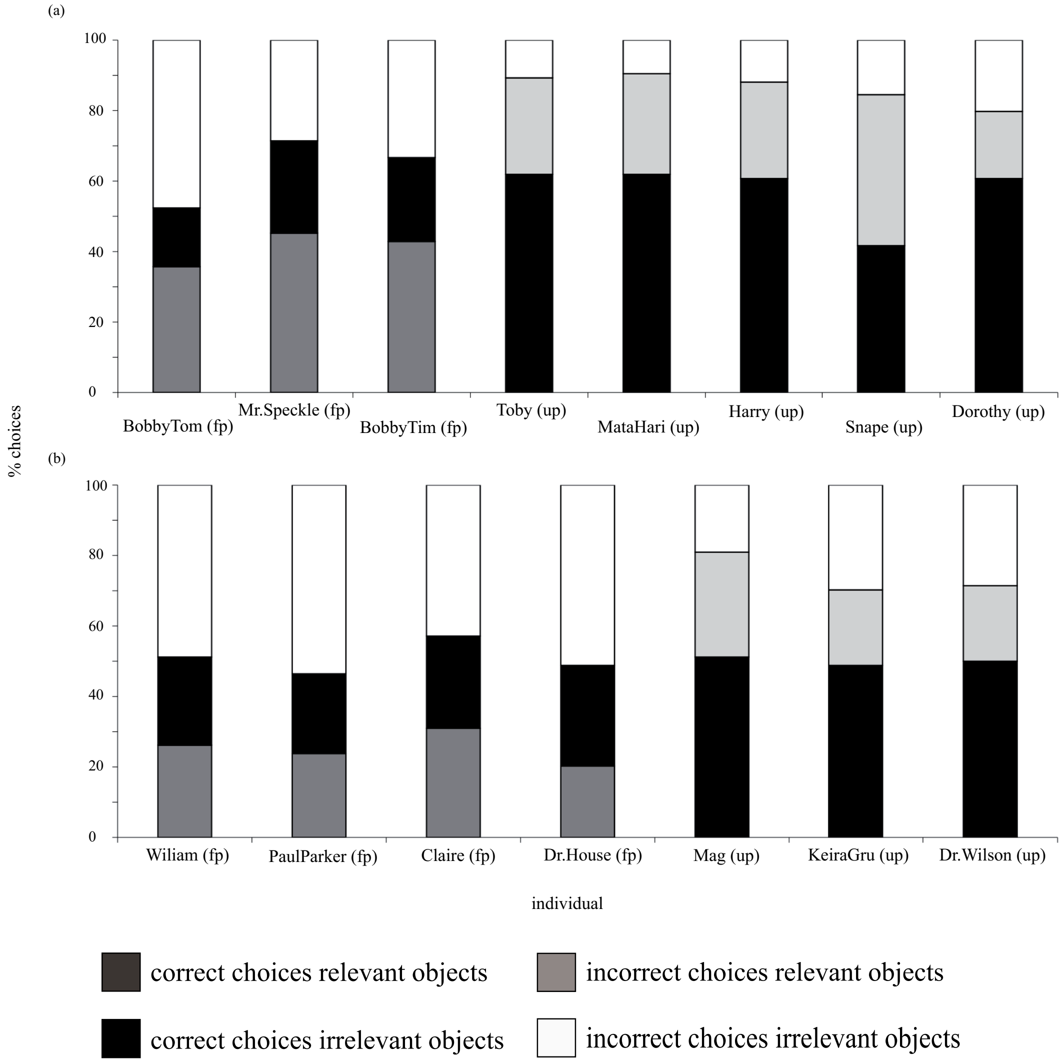

Figure 3 Detailed choice behaviour of experimental birds (a) and control birds (b) in the object familiarity test. Differently coloured proportions within stacked bars indicate correctness of choice and relevance of the chosen object. White parts: percentage of incorrect choices of “irrelevant” objects; light grey parts: percentage of incorrect choices of “relevant” objects; dark grey parts: percentage of correct choices of “relevant” objects; black parts: percentage of correct choices of “irrelevant” objects. Reward contingencies are represented by abbreviations behind subject names (fp= familiar positive, up= unfamiliar positive). Please note that for familiar-rewarded subjects, all incorrect choices were “irrelevant” (unfamiliar objects) and that for unfamiliar-rewarded birds all correct choices were all “irrelevant” (unfamiliar objects).

Table 1 Performance of all birds in the object familiarity test. Total numbers of correct and incorrect choices on relevant and irrelevant familiar objects are given. Column “correct vs. incorrect choices” shows p-values of the comparison between correct and incorrect choices on the basis of abstract familiarity. Column “relevant vs. irrelevant” shows p-values that were calculated from comparisons between the number of correct choices of relevant or irrelevant novel familiar objects for birds that were rewarded for familiar objects and the number of errors on relevant and irrelevant novel familiar objects for unfamiliar rewarded birds (please note that correct choices for unfamiliar-rewarded birds were always unfamiliar and thus irrelevant). P-values in bold indicate significance. All p-values are one-tailed and were revealed by binomial tests. Abbreviations in column “contingency”: fp = contingency familiar positive, up = contingency unfamiliar positive.

			correct choices		incorrect choices		correct vs. incorrect choices	relevant vs. irrelevant
			relevant	irrelevant	relevant	irrelevant		
experimental birds	Bobby Tom	fp	30	14	-	40	0.37	**0.01**
	Mr. Speckle	fp	38	22	-	24	**<0.001**	**0.03**
	Bobby Tim	fp	36	20	-	28	**0.02**	**0.02**
	Toby	up	-	52	23	9	**0.02**	**0.01**
	MataHari	up	-	52	24	8	**0.02**	**<0.001**
	Harry	up	-	51	23	10	**0.04**	**0.02**
	Dorothy	up	-	51	16	17	**0.03**	0.5
	Snape	up	-	35	36	13	0.08	**<0.001**
control birds	Dr. House	fp	17	24	-	43	0.46	0.17
	Wiliam	fp	22	21	-	41	0.46	0.5
	PaulParker	fp	20	19	-	45	0.29	0.5
	Claire	fp	26	22	-	36	0.12	0.34
	Mag	up	-	43	25	16	0.47	0.11
	Keira Gru	up	-	41	18	25	0.46	0.18
	Dr. Wilson	up	-	42	18	24	0.5	0.22

DISCUSSION

The results show that pigeons are able to discriminate between pictorial representations of objects on the basis of previous real-life experience with those objects. In the critical Object familiarity test, three quarters of the experimental group spontaneously classified objects that had not previously been seen as pictures on the basis of their real life aviary experience. This suggests that they transferred their real-life experience with the objects to the pictures thereof. Critically, none of the control birds passed this test, making it highly unlikely that perceptual features in the images controlled experimental birds' discrimination. In the Generalization test all pigeons were able to generalize to different viewing angles of objects they have been trained with, which proves intact generalization capacities on the basis of perceptual similarity in all subjects.

Pigeons are a typical prey animal and thus highly vulnerable to predators (Mueller & Berger, 1970; Palma et al., 2006, Stephan & Bugnyar, 2013). As an urban living species they are also thought to exhibit flexible learning strategies, which allows them to adjust their behavior appropriately to rapid environmental changes (Lee et al., 2011). Hence, the birds should be highly attentive to any newly introduced object, to learn whether it represents a potential threat or not. Accordingly, it is likely that the pigeons of the experimental group habituated to the introduced objects. Habituation clearly also involves perceptual learning and is considered beneficial (and thus relevant) in terms of decreased vigilance (which then allows the birds to increase other behaviors e.g. feeding time) and the avoidance of energetically costly flight behavior (Ydenberg & Dill, 1986).

Habituation also potentially involves associative learning of single objects. In particular, the consequences that arise from interaction with these single objects might well be learnt associatively. Logothetis and Sheinberg (1996) suggested that the recognition of external entities on the basis of abstract familiarity might require these entities to be somehow relevant for the receiver and to trigger the perceiving individual to be selectively attentive to them. However, categorization and in particular the formation of functional classes would require the birds to transcend independently learnt links between particular objects and consequences and to form equivalences across different objects beyond perceptual similarities.

Experimental birds could have used different mechanisms to recognize objects in photographs. Firstly, they could have formed mental representations of previously seen objects (Gärdenfors, 1995; Suddendorf & Whiten, 2001). This would require cognitive processes of recall that also comprise the flexible memorization of contextual information about the situation in which the memory of the object was formed. Secondly, the birds could have used unspecific "knowledge" of previous encounters with the objects without storing detailed contextual information that led to the formation of the functional class of "familiar objects" (e.g. Eacott & Easton, 2007). In the study presented here, pigeons were able to extract the abstract discriminative feature of previous real-life experience and showed no innate preference for familiar objects (denoted by similar acquisition phases and successful transfer in the object familiar test for unfamiliar-rewarded experimental birds). This indicates benefits resulting from habituation to known, non-threatening objects, supports memorization by means of familiarity and supports previous research that revealed no preference for familiar conspecifics in pigeons and chickens (Bradshaw & Dawkins, 1993). The discrimination of objects based on previous encounters alone does not require the memorization of specific contextual information about past individual interactions with this object. In contrast, the differential performance of the pigeons to relevant and irrelevant objects during the object familiarity test in the experimental group (in seven of eight subjects), but not the control group might hint at specific contextual knowledge about the objects. If familiar objects were characterized by an additional function that was "relevant" for the birds, pigeons seemed to selectively respond to these relevant familiar objects and hence transferred very specific knowledge about these objects to the discrimination of pictures, possessing a seemingly unlearned preference for "functional" familiar objects (Watanabe, 1993, 1996). This specific knowledge about relevant objects could not be based on object-inherent features alone but requires referring to past interactions with these objects in which this function was experienced. Again, none of control birds showed such preference for familiar objects that were supposed to be relevant. Furthermore, control birds that were rewarded for unfamiliar objects did not show a greater number of mistakes made on relevant familiar than on irrelevant familiar objects, as shown in the experimental birds. In sum, the performance of the control group makes it highly unlikely, that perceptual features in "relevant" familiar objects drove discrimination performance in experimental birds. One might argue that the effect of "relevance" might be due to the amount of time experimental birds spent with these objects and not to any function of objects. We do not claim that pigeons extracted any additional abstract feature of "relevance" and agree that different responses to relevant objects might also be due to the amount and frequency of interactions. But we think that exactly this difference in interactions indicates differences in the birds' interest in different objects, especially because experimental birds had free access to all introduced objects. That selective choices and preferences for objects, which were defined to be of any relevance to the birds, also resulted in significant effects on a group level makes it highly unlikely that individuals had random preferences for objects with which they spend more time and supports the claim that general object properties led to preferences in all experimental individuals.

However, whether birds actually recalled past sequences of interactions or formed additional functional classes of objects that were not only familiar but familiar and additionally functional, cannot be clarified with the present results. The results presented here suggest that familiarity with an object allowed learning, memorization and categorization of these objects but that inherent object properties associated with relevance influenced choice behavior (also indicated by a greater number of errors on relevant familiar objects by unfamiliar-rewarded birds in the experimental group, which might be due to low levels of inhibition).

Interestingly, recent studies on human preferences showed familiarity preferences for faces but novelty preferences for inanimate stimuli, like natural scenes (Park et al., 2010), although stimulus exposure and context of the task also seem to influence decisions (Crisp et al., 2009; de Vries et al., 2010; Liao et al., 2011).

We may only speculate about the individual differences among the birds' performance in the experimental group. These may point to differences in the frequency of interaction or the relevance of familiar objects for different subjects. Another interesting question would be whether it requires the birds to physically interact with the objects to be able to recognize them on the basis of abstract familiarity or if it is sufficient to observe others interacting as suggested for the learned avoidance of particular humans in crows (Marzluff et al., 2010).

If familiarity effects depend on the number and intensity of previous encounters with the depicted objects, individual differences may be even greater in the social context in which e.g. rank relationships, kinship or pair partners and thus potential relevance and frequency of interaction differ for almost each individual.

Thus, a whole variety of interacting factors might constitute the common consequence of "being familiar". In contrast, we expect inanimate entities to represent a promising alternative to address the ability to discriminate and generalize on the basis of familiarity and to experimentally identify underlying factors that influence the formation of this functional class.

An increase in the number of familiar objects and larger stimuli sets during the acquisition phase might also have facilitated the speed at which the experimental pigeons extracted the abstract rule and potentially also the number of individual birds that extract the common discriminative features among class members (e.g. Kirkpatrick, 2001; Cook & Wasserman, 2007). However, the present sets were large enough to enable the majority of experimental pigeons to extract the class-binding rule.

The fact that control and experimental birds showed similar learning rates suggests that it was equally demanding for all birds to acquire discrimination. This indicates that previous real-life experience had no facilitating effect on the number of trials that were needed to reach the acquisition criterion, although this might be also due to small data sample and the restricted number of different objects. However, the fact that experimental birds transferred the discrimination of familiar and unfamiliar objects to objects that had not previously been seen as pictorial stimuli whereas none of the control birds mastered the test indicates differences in the rule that birds applied for successful categorization at the end of the training phase. Although speculative, learning perceptually complex man-made objects by rote in control birds might be equally demanding as extracting the discriminative feature by referring to individual pre-experience with presented objects in experimental birds. As a result, both groups needed comparable exposure to training stimuli for reliable discrimination but might have learned using different rules. In conclusion, previous real-life experience with objects may not lead to faster reliable discrimination of pictures thereof but may trigger the birds' attention towards other features than those used for discrimination by birds without this real-life experience.

The categorization of pictorial stimuli that is based on individual pre-experience is also a promising approach to further investigate picture-object recognition in animals. Although the transfer of discrimination from real objects to pictures as suggested by Weisman and Spetch (2010) might give first hints to perceived equivalence of both presentation modes, the birds could potentially also use 2-D features that are present in both objects and pictures to accomplish the task. In contrast, if birds are only provided with the discriminative feature during real-life interactions, they have to refer to this experience with real objects to successful categorize also pictures thereof.

In conclusion, our results showed that (a) pigeons are able to discriminate pictures of inanimate objects on the basis of whether they have encountered those objects in real life before and (b) that this discrimination is likely to be affected by whether those objects had any additional function or not. Furthermore, the present results give further empirical evidence of picture-object recognition and representational insight in pigeons (Aust & Huber, 2006, 2010).

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ETHICAL STANDARDS

All subjects that participated in reported experiments are housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act – TSchG, BGBl. I Nr.118/2004). Furthermore, as the present study was strictly non-invasive and based on behavioral observations, all experiments are classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 501/1989).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Figure A1 Pictorial presentations of objects. Two (out of 14) exemplars of different viewing angles are shown for each object.

CHAPTER 4: HAVE WE MET BEFORE? PIGEONS RECOGNISE FAMILIAR HUMAN FACES.

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ABSTRACT

Despite growing evidence for the recognition of conspecifics, studies on heterospecific recognition are still scarce. There is some evidence that birds living in urban habitats are able to distinguish between specific humans, depending on their previous experience with them. Nonetheless, the features by which the birds actually discriminated among humans remain unclear. This study investigated whether pigeons are capable of performing such a sophisticated categorization and the features relevant to making this discrimination. The results revealed that pigeons are able to reliably discriminate between familiar and unfamiliar humans and provides evidence that facial features are important for this recognition. Furthermore, our results suggest that the ability to discriminate between individual heterospecifics is not restricted to bird species that are considered highly cognitive.

Keywords: *Columba livia*, concept of familiarity, heterospecific recognition, human face recognition

INTRODUCTION

Several animal species are able to discriminate between subcategories of conspecifics (e.g. Levey et al., 2009; Tricarico et al., 2011). However, evidence for the recognition of individuals, or classes of individuals, among heterospecifics is scarce. Interestingly, most studies of heterospecific recognition have either focussed on predator recognition or on the recognition of humans by either farm animals or by wild animals in urban environments (e.g. Slobodchikoff et al., 1991; Munksgaard et al., 1997; Taylor & Davis, 1998; Ferrari et al., 2008; Stone, 2010; Bogale et al., 2010).

Many animal species living in human environments benefit from reduced predation rates, year round food availability and new opportunities for breeding sites. Although food is largely available throughout the whole year, animals have to learn to exploit multiple different food sources. Consequently, if individuals flexibly adjust to many different circumstances in various locations, foraging becomes less costly in terms of searching and handling time. Nonetheless, the presence of specific humans may represent a potential threat, especially if a species is regarded as a pest. This suggests that the recognition of individuals beyond species borders may be facilitated by the ecological need to memorise individual features of heterospecifics. Accordingly, urban bird species like magpies, mockingbirds and crows have been reported to discriminate and remember humans based on their previous experience with them (Levey et al., 2009; Marzluff et al., 2010; Lee et al., 2011). The explanations for such advanced discrimination abilities are twofold. On the one hand Marzluff et al. (2010) have suggested that corvids are predisposed for rapid learning because of their high general cognitive abilities. On the other hand, it could be argued that species that live in human areas and that are frequently exposed to many human individuals benefit if they can recognise individually distinct features and adjust their behaviour accordingly. This “pre-exposure” hypothesis, proposed by Lee et al. (2011), suggests that all urban living species with much exposure to humans should rapidly learn to discriminate among humans, depending on their pre-experience with those particular individuals. Although both hypotheses are not mutually exclusive, recent studies with pigeons challenge the idea that these advanced recognition abilities predominately occur in species with ‘higher cognitive’ abilities. Belguermi et al. (2011) revealed that foraging feral pigeons spatially avoid human feeders that had previously shown hostile behaviour (*e.g.* arm waving or chasing) during foraging. Further, Dittrich et al. (2010) showed that pigeons react with higher levels of activity whenever the person that usually fed the birds entered the housing environment but responded less when individual humans wore masks, indicating that facial cues served as reliable discrimination criterion. Nonetheless, when the pigeons were asked to transfer the recognition of their real-life feeder to 2D-images of the latter, the birds completely failed to distinguish familiar from unfamiliar humans.

Despite this negative result, the presentation of photographic images can still be considered advantageous. Previous studies revealed that birds could discriminate between conspecifics (Nakamura et al*.*, 2003; Wilkinson et al*.*, 2010) although the exact discriminative features remain unknown (Ryan & Lea, 1994). There is also evidence that they can discriminate heterospecifics (e.g. Marzluff et al., 2010). Dittrich et al. (2010) emphasised the importance of human facial cues for discrimination whereas other studies indicated a facilitating effect of different clothing or acoustic cues on discrimination (Belguermi et al*.*, 2011; Sliwa et al*.*, 2011; Wascher et al., 2012). Consequently, the use of pictorial representations offers the opportunity to restrict and select all cues given during discrimination.

In the present study we investigated the pigeon's ability to recognise familiar heterospecifics, namely humans, when only presented with pictorial representations of facial features. We used the familiarity discrimination acquired in a previous experiment (Stephan et al., submitted) that used objects as stimuli and examined the impact of different stimulus properties that influence concept application. The focus of the experiment presented here laid on whether pigeons could transfer this to novel stimuli that are perceptually very different and with which the birds had a very different kind of pre-experience than with the objects.

Although the use of objects during the training might appear somewhat bewildering, it emphasised the main aspect of the present study, namely the extent to which the birds are able to transfer the abstract concept of familiarity when confronted with completely different stimuli. The object discrimination study investigated the factors that trigger the application of this concept. By using objects during the training we were able to control for any perceptual cues in the human faces that might have triggered classification on this basis rather than that of familiarity. The experiment was designed to exclude any basic forms of social learning e.g. observational learning, which is likely to influence the birds' responses (Marzluff et al., 2010). This was made possible by testing the birds individually in an operant chamber. We restricted the stimuli so that only visual information of human faces was available; this allowed us to disentangle the impact of facial cues for recognition from additional features.

METHODS

Subjects

Fifteen homing pigeons were assigned to either a control (N = 7) or an experimental group (N = 8). The entire group of experimental birds lived together in an outdoor aviary (2.9 x 2 x $3m^3$), as did all birds of the control group (2 x 1 x $2m^3$). The aviaries were visually isolated from each other. Both aviaries contained perches, nesting boxes and a water dispenser. Water and grit were freely available throughout the whole experiment whereas food was only provided during experimental sessions and over the weekend. All birds were maintained at 90% of their free feeding weight.

Stimuli

Real Objects and Humans

Within the training phase, birds were presented with photographs of objects (of various kinds, including various colours, shapes and sizes; e.g. a kettle, a torch, a fork, sunglasses, etc.; for examples please also see Fig. 1) that were either familiar to the experimental group or completely unknown to both groups of birds. Two weeks prior to the first training session the familiar objects were placed either in the aviary of the experimental birds or in the aviary opposite the experimental group (so they only had visual access to them). All of the familiar objects remained *in situ* throughout the experiment. The control birds could not see or interact with any of these objects.

For the Human Faces Familiarity test, eight people were photographed; four were in frequent contact with the pigeons and four had never been in physical or visual contact with them. Interaction with the familiar people included cleaning, feeding and capturing of the birds. The minimum criterion for a person to be familiar was either to interact with the birds (e.g. feeding or catching them) at least twice a week or to enter the aviary on a daily basis for at least five minutes.

All of the objects were unfamiliar to control birds but all birds had seen the familiar humans before. In the critical test, control birds should not be able to successfully discriminate between familiar and unfamiliar human faces, as they will not have acquired the underlying logic of the task during the trainings phase.

Photographic Stimuli

During the acquisition phase, pigeons were presented with photographs that showed different objects (Fig. 1a). Photographs were taken of 16 familiar and 16 completely unknown objects and were controlled for colour, shape and size. Fourteen photographs of each object were taken from at least 10 different angles.

In the Human Face Familiarity test, all photographs showed only the head and part of the neck (Fig. 1b). Photographs of humans depicted four familiar and four unfamiliar humans. Again, fourteen photographs were taken from at least 10 different angles and included both sexes. There were no discriminative features shared between the objects and human faces in general or between familiar objects and familiar human faces (e.g. overall shape, colour).

All pictures were taken under different light conditions and the same stimulus was photographed under both indoor and outdoor lighting. Photographs were presented on a touchscreen in an operant chamber. During stimulus presentation all photographs were displayed at a size of 3.8cm x 3.8cm. All pictorial representations of objects and human faces were modified and presented on a homogenised background colour using PhotoShop software package (© Adobe Inc.). Thus, any salient background features were excluded. The background colour was chosen to provide the highest level of contrast to all stimuli.

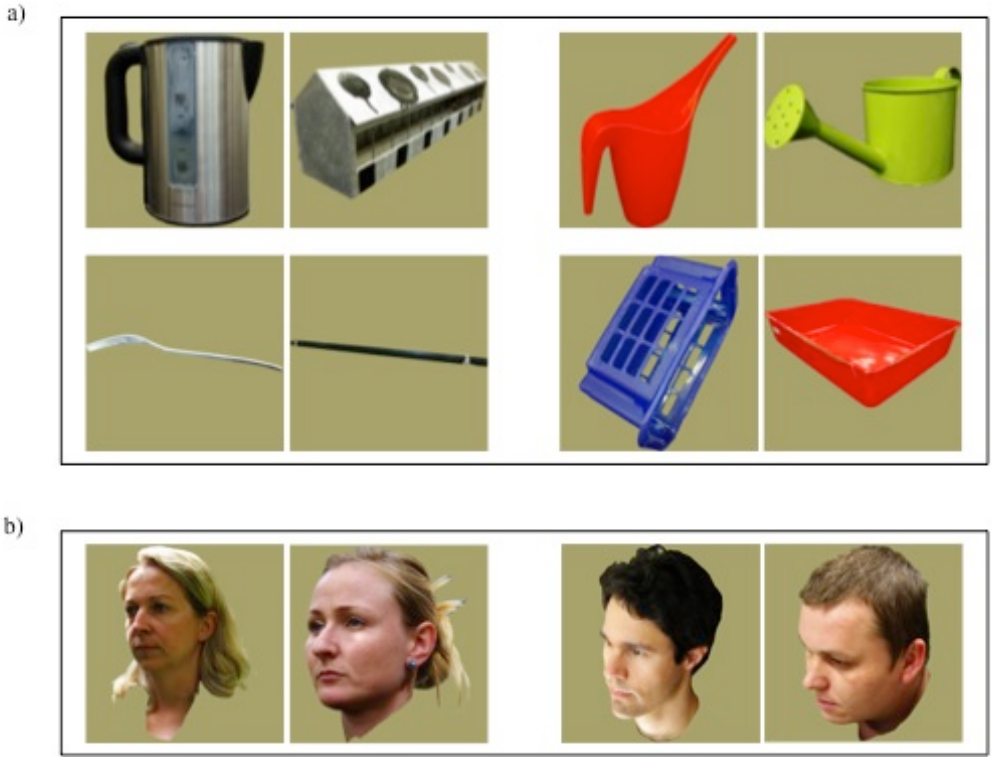

Figure 1 Examples of the familiar and unfamiliar stimuli shown during a) the acquisition phase (objects) and b) the face familiarity test (human faces). The right stimulus of each pair represents a familiar stimulus, the left one an unfamiliar. Across stimuli, various perceptual differences were controlled for (*e.g.* for objects: shape, size, colour, light conditions and for human faces: sex, hair colour, orientation of the head and light conditions).

Apparatus

The entire experiment was carried out in Skinner Boxes, measuring 50cm x 30cm x 40cm. An infrared touch frame was mounted in front of a 15 inch monitor at one end of the box and a piston (lifted by a motor unit after each correct response) provided food. The feeder system and touch screen presentations were controlled by a specialist software package ("CognitionLab", M. M. Steurer).

Procedure

Discrimination training

The pigeons had already been trained to discriminate between familiar and unfamiliar objects (Stephan et al., submitted) and this experiment extended this by investigating whether they could generalise the learning about objects to novel stimulus forms (faces). The object training consisted of presentation of photographs of ten familiar objects and ten unfamiliar objects. The pigeons were trained using a two-alternative forced choice procedure in which two photographs were presented on a touch-screen computer monitor, one positive and one negative. Pecking at the positive stimulus led to an auditory signal, the screen clearing and 3s access to food. Choice of the negative stimulus led to a different auditory signal, the screen flashing red (3s) and a correction trial (a repeat of the same trial). This continued until the positive stimulus was selected. Each trial was separated by an inter trial interval of 6 seconds; during this time the screen was dark. Reward contingencies were counterbalanced, so half of the experimental group were rewarded for choosing the familiar object and half for choosing the unfamiliar one. To ensure that there were no perceptual cues in the images each control bird was presented with identical stimuli and contingencies as a corresponding experimental bird.

Each training session comprised 50 trials. The acquisition criterion was met when a pigeon made correct first choices in 80% of the trials (40/50 trials) in four out of five consecutive sessions and at least 75% (38/50) in the remaining session. As the subjects had previous training on this task (for training performances see Fig. 2) all subjects reached criterion again within a maximum of 12 training sessions.

Human faces familiarity test

After the birds reached the acquisition criterion, they were presented with a critical test in which we investigated whether the pigeons were able to transfer their learned discrimination to human face stimuli. Test trials which contained human faces were pseudo randomly intermixed with the object training trials. There was no test trial at the start and at the end of each session and test trials could not appear in a row. One of the human faces was familiar to the pigeons and the other one was not. Pecking at the familiar or the unfamiliar human face indicated the choice behaviour of pigeons. Within each test session, eight test trials were randomly intermixed with 50 training trials, resulting in 58 trials per session. If the birds did not respond to criterion on the training trials that were intermixed with the test trials the session was repeated. There was no differential feedback in test trials, meaning that both stimuli disappeared after the first peck was emitted, independently of whether the choice was correct. A total of 56 different test trials were presented to each bird, distributed among 7 test sessions in total. Although both the experimental and control birds were familiar to the humans, it was predicted that only the experimental birds should categorise the faces correctly as the control birds did not have any visual experience with familiar objects and thus could not (and did not) learn the initial familiarity discrimination. They were, therefore, expected to perform at chance during this test, pecking randomly at one of the two presented human faces.

Data Analysis

The discrimination performance was assessed by means of two-tailed binomial tests. All statistical analysis was conducted in SPSS v.17.

RESULTS

On a group level, birds of the control group required a median of 36 (range: 25 - 70) sessions to reach criterion whereas experimental birds reached the acquisition criterion in a median of 28 (range: 26 - 42) sessions (Fig. 2). However, this apparent difference was not significant. The results of the Human Faces Familiarity test revealed that four out of eight experimental birds successfully categorised pictorial representations of human faces on the basis of familiarity and, critically, all control birds failed (for individual performances please see Table 1).

Throughout the test sessions all birds in experimental and control group maintained their highly significant performance in training trials. Thus the birds had not been disturbed by the presentation of perceptually very different stimuli during test sessions.

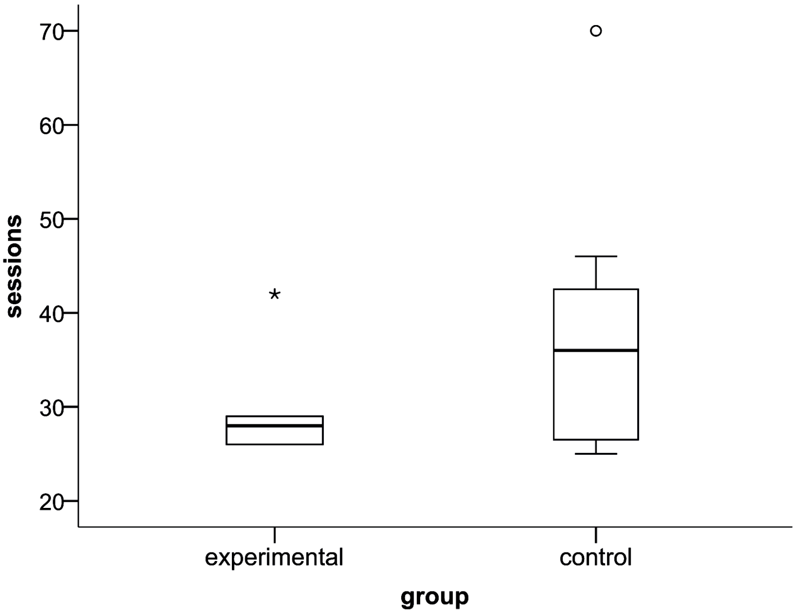

Figure 2 Number of sessions to reach acquisition criterion for experimental and control group. Boxplots include the median, first and third quartile and extreme values (circle and asterix).

Table 1 Individual performances in the discrimination of familiar and unfamiliar human faces. Significant classification is indicated by p-values in bold and was assessed by means of two-tailed binomial tests. The level of significance was set to $P < 0.05$.

Pigeon name	$N_{\text{correct choices}}$	$N_{\text{incorrect choices}}$	P-value
Experimental Group			
Bobby Tom	29	27	0.894
Dorothy	28	28	1
Bobby Tim	37	19	**0.022**
Toby	39	17	**0.005**
Mata Hari	43	12	**< 0.001**
Harry	42	14	**< 0.001**
Mr. Speckle	34	22	0.141
Snape	30	26	0.689
Control Group			
Dr. Wilson	33	23	0.229
Claire	23	33	0.229
Wiliam	26	30	0.689
Mag	29	27	0.894
Keira Gru	31	25	0.504
Dr. House	21	35	0.081
Paul Parker	29	27	0.894

DISCUSSION

The present results show that some pigeons are able to recognise and correctly classify individual heterospecifics on the basis of facial information. Moreover they were able to do this when the human faces were presented as photographic stimuli and only 2D-information was available. Four out of eight pigeons in the experimental group succeeded in correctly classifying the pictures even though the birds were not previously trained with familiar and unfamiliar human face stimuli. Critically, all subjects of the control group failed to discriminate familiar from unfamiliar human faces in the transfer test revealing that a perceptual rule or preference did not underlie the successful performance of the experimental group.

All the birds were trained on photographs of objects, half of which were familiar and half unfamiliar to the experimental group (both were unfamiliar to the control birds). The training was part of a previous experiment that investigated the pigeons' ability to discriminate individual objects on the basis of familiarity and the object features that were important for concept formation. In the present experiment, we wanted to investigate whether the birds could transfer the complex discriminative rule of familiarity to heterospecifics. The fact that control birds saw familiar humans, as did the experimental birds, but were not able to classify them reliably, supports the interpretation that pigeons acquired the abstract feature of familiarity for discrimination. Consequently, all control birds mastered the training by rote learning and thus showed random choice behaviour in the critical test.

In contrast to previous studies (e.g. Dittrich et al*.,* 2010; Belguermi et al., 2011) we did not artificially manufacture encounters with specific humans involving exclusively negative or positive events. In fact, two of the familiar humans captured, released and fed the birds on a regular basis, one was only involved in cleaning the aviaries and one was entering the aviaries but not handling the birds directly. Thus the present results suggest that in a long-term relationship between pigeons and humans, the memorisation and recognition of humans is not necessarily mediated by previous interactions that have been explicitly hostile (e.g. catching) or friendly (e.g. feeding). Given the context of encounters and long-term exposure to humans, we can exclude fear conditioning and predator avoidance as mechanisms of recognition (Griffin, 2004; Marzluff et al*.,* 2010). For the birds tested here, humans appear to be relevant in a broad sense and this may be sufficient to maintain recognition of the subset of humans that interact with the birds on a regular basis. Hence, this study provides support for the impact of visual pre-experience in facilitating the recognition of ecologically relevant heterospecifics (Marzluff et al., 2010; Lee et al*.,* 2011). For the successful discrimination of familiar humans, pigeons had to separate features that are constant within individual humans over several encounters (e.g. facial cues) from those that vary and/or overlap considerably between humans (e.g. clothing, movement, body size). Marzluff et al. (2010) already found a strong indication that crows paid attention to peoples' faces and suggested that these features might provide a valuable discriminative feature as they vary little within a human but reliably vary between humans. The present results suggest that facial information alone is sufficient for pigeons to discriminate among humans, although the exact features that are used to do this still need to be identified.

As pigeons are not known for their abstract cognitive abilities but possess extraordinary visual discriminative abilities (e.g. Huber et al., 2000; Aust & Huber, 2006; Huber, 2010; Huber & Aust, 2011;), it seems unlikely that pigeons are predisposed for rapid learning by their high cognitive abilities as has been suggested for corvids (Emery, 2006). Instead we suggest that for some species, the extensive exposure to ecologically relevant heterospecifics might be sufficient for cross-species individual recognition on a class level. At least for pigeons, urban living or captive care may meet this prerequisite.

Although experiments that are conducted on wild populations have the advantage of exploring behavioural responses under natural conditions, controlled experimental conditions provide the opportunity to systematically restrict and control the information given to individual animals. By training our pigeons under controlled captive conditions we were able to manipulate both their real-life experience with the training stimuli (objects) and the test stimuli (humans). We were also able to prevent the control birds from acquiring the crucial discriminative feature by ensuring that they had no visual access to familiar objects. Simultaneously, we used a variety of objects with very different appearance during the training to facilitate the transfer of discrimination (Cook et al., 1990) and controlled for similar amounts of pre-experience with every object among the experimental birds. Hence, we consider studies on captive birds to provide a promising approach to further investigate the exact impact of pre-experience on heterospecific recognition although obtained findings must be tested in the field to evaluate the ecological relevance of this capacity under natural conditions.

In conclusion, pigeons are able to recognise familiar humans on the basis of 2D-representations of facial features. In contrast to corvids, pigeons are not thought to be genetically predisposed to show high-level cognitive abilities. Nonetheless, extensive experience with heterospecifics, the ecological need to recognise individuals and to adjust their behavioural response on the basis of this may lead to comparably sophisticated cognitive capacities and represent a surprisingly flexible learning capacity. The extent of these abilities is currently unknown. Whether the birds possess “true” individual recognition of heterospecifics is unclear and investigations of cross-modal recognition would be a promising focus for further studies.

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CHAPTER 5: HOLOGRAPHY AS A NOVEL TOOL FOR INVESTIGATING 3D-INFORMATION PROCESSING: DISCRIMINATION OF HOLOGRAMS AND REAL OBJECTS BY PIGEONS AND HUMANS

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ABSTRACT

The type of stimulus material employed in visual tasks is crucial to all comparative cognition research that involves object recognition. There is considerable controversy concerning the use of 2D stimuli and the impact that the lack of the 3rd dimension may have on pigeons' performance in tests for their visual and cognitive abilities. Here, we report, for the first time, evidence of discrimination learning with a completely novel type of stimuli, namely holograms. Like real objects, holograms provide full 3D shape information while, at the same time, they offer many possibilities for systematically modifying the appearance of a stimulus. For that reason, they provide an innovative and promising means for investigating visual perception and cognition of different species in a comparative way. Pigeons and humans were trained to discriminate either between two real objects or between holograms of the same two objects and were subsequently found able to transfer that discrimination to the other presentation mode without any decrements in accuracy. This suggests that real objects and holograms were indeed perceived as equivalent and shows the general appropriateness of holograms as stimuli in visual tasks. A follow-up experiment that involved the presentation of novel views of the training objects and holograms revealed some inter-species differences in rotational invariance, thereby confirming and extending the results of previous studies. Thus, holograms may not only provide a promising tool for investigating yet unexplored issues, but their use may also lead to new insights into some crucial aspects of long-standing questions in comparative visual perception and categorization that have, so far, been studied only with traditional stimulus presentation techniques.

Keywords: holograms, objects, rotational invariance, categorization, humans, pigeons

INTRODUCTION

The strategies chosen by pigeons and their success in visual categorization tasks have repeatedly been shown to be affected by the information that the birds' perceive in and infer from used stimulus material (e.g. Herrnstein, 1985; Huber et al., 1999). Empirical data suggest a considerable impact of e.g. colour and texture (e.g. Huber et al. 2000; Aust & Huber, 2001, 2010; Aust & Steurer, 2012), acoustic cues (Partan et al., 2005) and information provided by the 3rd dimension (Dittrich et al., 2010).

The majority of previous studies used complex pictorial images as stimuli to address pigeons' visual discriminative abilities. Although pigeons have proved able to discriminate complex patterns and representations of objects in two-dimensional visual scenes (for reviews see, e.g. Huber, 2000; Lazareva & Wasserman, 2008; Zentall et al., 2008), they seem to have difficulties in tasks that require more abstract inferences. For example, they have repeatedly failed in tests for amodal completion of partly occluded objects (e.g. Sekuler et al., 1996; Fujita, 2001a, b; Ushitani et al., 2001; Aust & Huber, 2006a) or the assessment of structural information from motion cues (e.g. Loidolt et al. 2006). However, both abilities would, without doubt, be advantageous and therefore of adaptive value also for pigeons (e.g. Dittrich et al., 1998, Dittrich & Lea, 2001; Fujita & Ushitani, 2009). The reasons for such previous failure are actually twofold. Either subjects do not possess the tested discriminative or cognitive abilities that would enable them to succeed or the methodology, namely the presentation of pictures instead of real objects, does not provide them with all information that is necessary for recognition and thus successful categorization. For studies in which e.g. pigeons reliably discriminated real humans but failed to successfully categorize pictures of these humans (e.g. Dittrich et al., 2010), it remains unclear whether the birds are limited in their cognitive and discriminative abilities or whether they used discriminative features that were present in real humans but not in pictures thereof. In general, pictures are always abstractions of their 3D-referents (Bovet & Vauclair, 2000; Fagot, 2000). As a consequence, they lack or misrepresent features that normally support object recognition. For example, pictures do usually not provide motion and they lack information about the 3rd dimension. More specifically, although pictures do contain at least some cues that enable humans to infer depth (provided, for example, by shadows), it is not clear how animals may perceive and interpret such cues. Indeed, pigeons' repeated failure to perceive unity of partly occluded objects and their occasionally reported difficulties to derive structure from motion — which both require the perception of different "layers" in depth — suggests that their ability to infer 3D-cues from 2D-stimuli may be strongly limited. Moreover, pictures have traditionally been produced and presented with technology that is adapted to human vision and ignores potential differences to other species' perceptual systems (Delius et al., 2000). In particular, pictures often lack some critical features of birds' vision, e.g. UV-light, and offer false color representations because of the tetra- or pentachromatic vision of birds (Bowmaker, 1980; Emmerton & Delius, 1980; Emmerton, 1983; Emmerton & Remy, 1983; Bowmaker et al., 1997; Delius et al., 2000). Furthermore, restricted spatial and temporal resolution, poor luminous and chromatic replication, and flicker frequency of computer monitors must make pictures appear quite different from natural objects to nonhuman animals (for studies using video presentations see e.g. D'Eath, 1998; Ikebuchi & Okanova, 1999).

In attempting to bypass the problems associated with pictorial stimuli several studies have used real objects instead (e.g. Friedman et al., 2005; Spetch & Friedman, 2006). However, the use of real objects also bears some disadvantages. First, the physical properties of objects may change over time (e.g., due to mechanical damage, dirt, or continued exposure to light). Second, systematic variations of particular stimulus properties (like color or size) may be difficult if not impossible to realize with real objects.

The experiments reported here introduce an innovative stimulus presentation technique, namely holography. It combines the advantages of pictures and real objects while avoiding many of their shortcomings. Holograms have so far not been exploited in studies on animal cognition, although considerable benefit can be expected from using such types of representations. For visual perception, they provide full physical information of a stimulus (like real objects), but nevertheless allow for flexible manipulation of individual stimulus features (like computer images). While the light as it comes from real objects is specified not only by its amplitude and wavelength but also by its phase, phase information is lost in photographs, and with it directional information and thus the 3D-effect. Holograms, by contrast, allow for retrieving depth information by recording not only the intensity of the incident light onto a photographic film, but also its phase. This is accomplished by a recording being captured as an interference pattern at the film. This means that highly coherent light from a laser is scattered by the surface of an object and then interferes with non-scattered light from a reference beam. This technique permits recording and displaying the complete information contained in a wave field. By replaying the wave field from a hologram, 3-dimensional viewing of the recorded object becomes possible (for details on holography see, e. g. Bally, 1979; Hariharan, 2002; Ackermann & Eichler, 2007 and appendix). Thus, when perceived visually, holograms provide the same physical information as objects about the 3rd dimension, which makes them a powerful means for investigating the extent to which the 3rd dimension supports object recognition. With rotating holograms, it would even be possible to investigate motion effects (like structure-from motion; e.g. Dittrich & Lea, 1993; Jitsumori et al., 1999; Mascalzoni et al., 2009).

With the present study, we aimed to introduce holograms to comparative visual perception and cognition research. We consider the usage of holograms to be of particular interest and benefit for all studies that investigate object recognition in animals and the discriminative features that are used for this. Also picture-object equivalence might be addressed with a greater variety of features that may be modified more easily in holograms than in 3D-stimuli. However, the very first step in the establishment of holograms for the investigation of object recognition is to show hologram-object equivalence. This equivalence in the physical information that is provided by objects and holograms should lead to equivalent perception and equivalent performances on both and represents the prerequisite for full object replacement. As soon as holograms have been established to replace real objects, they provide a promising alternative in studies on visual cognition, including, for example, experiments on picture-object equivalence, amodal completion, or structure-from motion.

The experiments reported here applied a comparative approach by testing the discriminative abilities of humans and pigeons. Although they stem from different reptile clades that went separate evolutionary ways some 310 million years ago (Kumar & Hedges, 1998), pigeons and humans still face some similar challenges when it comes to the computation of visual information. For example, as highly visual and mobile species they both have to be able to integrate information across various viewpoints or to select the most relevant features, like cues for conspecific recognition, to adjust behavioural responses appropriately (e.g., Partan et al., 2005; Wilkinson et al., 2010). Hence, the comparative investigation of visual perception in pigeons and humans provides a promising approach to broadening our knowledge on the perceptual and cognitive similarities and differences that might have evolved in parallel in species with different phylogenetic histories.

In the present study subjects of both species were trained and tested with a novel, custom-made apparatus that had been developed for the presentation of various kinds of stimuli, including holograms and real objects (Steurer et al., 2012a). Pigeons and humans were confronted with the same visual discrimination task that required them to distinguish between two nonsense figures (“Greebles”), presented either as holograms (Group Hologram) or as real objects (Group Object) and were then tested for transfer to the other presentation mode (Experiment 1). Subsequently, the suitability of holograms in tests for transfer to novel views of training stimuli (i.e. rotational invariance) was investigated, with a particular focus being laid on possible differences between the two species (Experiment 2).

Experiment 1: Hologram-object equivalence

INTRODUCTION

Experiment 1 was aimed at investigating whether pigeons and humans would perceive real objects and holographic images as equivalent, thereby evaluating the appropriateness of the latter as stimuli to be used in visual discrimination tasks. To this end we trained pigeons and humans to discriminate either between real objects (Group Object) or between holographic images derived from the latter (Group Hologram). When the subjects had acquired the task, they were tested for transfer to the other presentation mode.

METHOD

Subjects

Pigeons

Twelve pigeons of a local Austrian strain (Columba livia Strasser) served as subjects. They were kept in an outdoor aviary (2.7m x 1.2m x 2.94m; length x width x height), equipped with nesting boxes, perches, and a water dispenser. Water and grit were available at any time whereas food was provided only during and immediately after experimental sessions and at weekends. All birds were maintained at about 90% of their free feeding weight. The subjects were arbitrarily assigned to two different groups, defined by the mode of stimulus presentation during training. Group Object ($N = 6$) was trained with real objects; Group Hologram ($N = 6$) was trained with holographic images of the same objects. None of the pigeons had participated in visual discrimination tasks with the present stimuli before, but some of the subjects had previously participated in unrelated visual discrimination tasks in a touch screen set-up.

Humans

Ten humans (3 men, 7 women, ranging from 20 to 46 years of age) were assigned to the same two groups as the pigeons (Groups Object and Hologram), with each group consisting of 5 subjects. None of them had ever participated in a visual discrimination experiment before. All subjects had normal or corrected-to-normal vision.

Apparatus

The experiments were carried out in a custom-built operant chamber *(Multi-Stimulus Box; MSB)*, which allows for the flexible presentation of various stimulus types, including real objects and holograms (Fig. 1; for details see Steurer et al., 2012a). The external measures of the apparatus were 90cm x 150cm x 146cm (depth x width x height). It rested on aluminum posts with wheels for moving the apparatus (if necessary), and the entire MSB was covered with plastic panels to protect the interior from dust and dirt. A mobile Skinner box (53cm x 42cm x 45cm; depth x width x height) was adjoined to the frontal wall of the MSB, which contained a panel with a transparent response key (∅ 5cm). For humans, the Skinner box was replaced with a cabin consisting of a metal frame that was covered with black, opaque fabric (110cm x 100cm x 200cm; length x width x height). Furthermore, the response key (which was the operandum for pigeons) was removed, as human participants had to respond by pressing a button. Instead, a panel was inserted that provided them with equal visual access to the stimuli as the pigeons.

The stimuli to be presented were attached to “slots” that were mounted onto two vertically rotating wheels. The front wheel (from the subject’s point of view) could be loaded with holograms, whereas the back wheel carried the objects (Fig. 1). Each wheel provided nine slots for attaching stimuli. However, one slot had to remain empty on every trial in order to avoid visual overlaps between stimuli placed on the front and the back wheel. Thus, a maximum of eight different stimuli per session could be shown on each wheel (for examples see Fig. 2a). Stimuli could be exchanged between sessions, thereby (potentially limitlessly) increasing the number of stimuli that could be shown in the course of an experiment. The two wheels were controlled by separate engines and, prior to each trial, brought the next stimulus to be presented into a position that allowed the subject to view it through the response key. The duration of wheel rotations was varied from trial to trial by adding extra rotations, in order to prevent the subjects from attending to spurious temporal patterns. Furthermore, it was made sure that holograms (front wheel) projected onto the same spot at which the objects (back wheel) were shown. The gap between stimulus and response key was bridged by a 15cm viewing tunnel with opaque walls that restricted the subjects' viewing angle and thus prevented visual access to neighbouring stimuli on either wheel. Also, the walls restricting the viewing angles under which the holographic image could be seen ensured them being perceived without distortion: The viewing tunnel ensured a minimum distance between the observing subject and the presented stimuli, and the maximally possible opening angle of the reproduced wavefront was larger than the viewing angle that could be achieved in the box. Thus, although our subjects could vary the position of their heads and thus the viewing angle, it was not possible to exceed the opening angle of the reproduced wave front. This allowed for hologram inspection under all possible viewing angles without the images appearing distorted. A black roller blind behind the object wheel provided a homogenous (and identical) background for all stimuli. A shutter behind the response key (or, for humans, in front of the panel) was closed between trials (and raised again at the onset of stimulus presentation) so that the subjects were unable to observe any changes of stimuli and/or settings during the intertrial interval. Reward for the pigeons was administered by an automated feeding device that lifted a piston with a depression on top through a food reservoir. Through a hole in the bottom of the box grain trapped in the depression was made accessible to the pigeons for 5 seconds after a correct response (for details see Steurer et al., 2012b).

Holograms and objects were illuminated by a green diode-pumped solid-state laser (DPSS) with a wavelength of 532nm. The laser and all associated laser device electronics were housed in a special case. All experiments were controlled by a custom-built computer that integrated feeder control and data registration via the response key (or the response button, respectively), and a special software package (Steurer et al., 2012b).

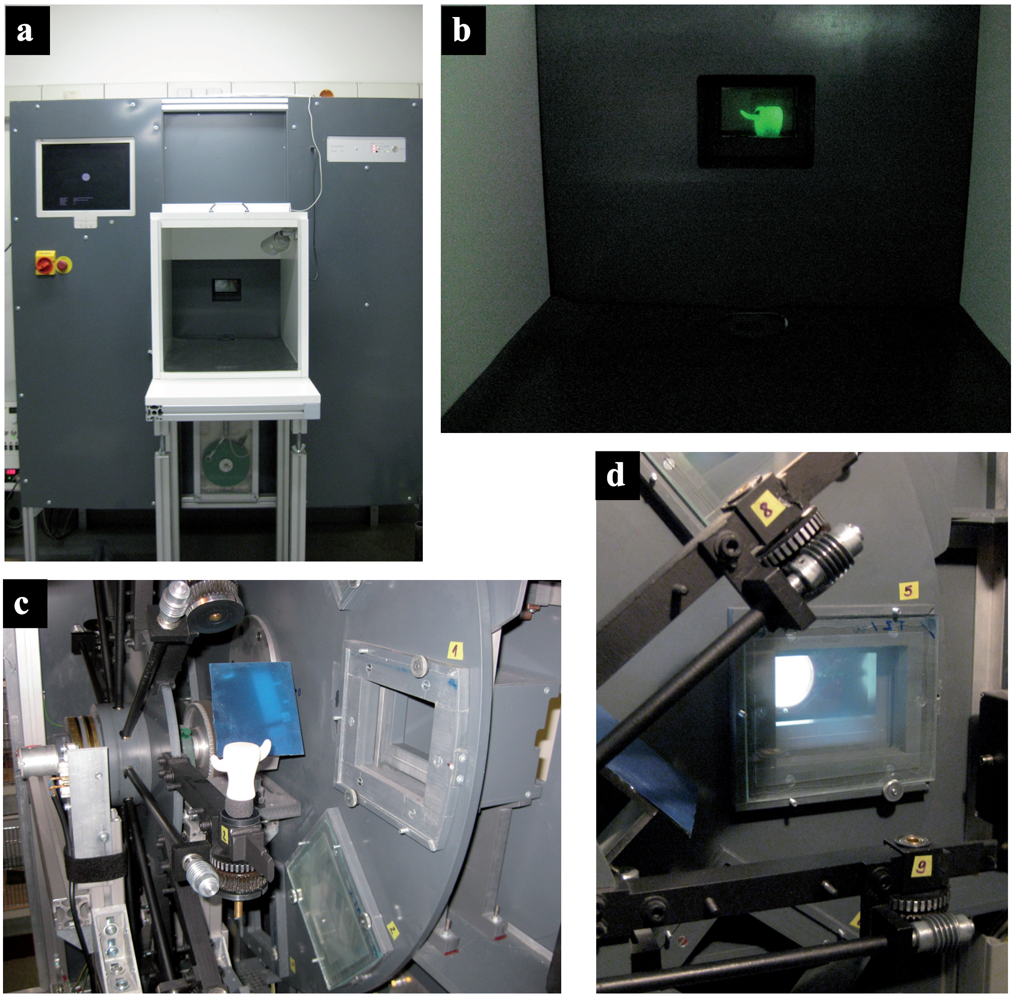

Figure 1 Photographs of the apparatus. a) Outside view of the MSB (rear wall of Skinner-box removed); b) Interior of the Skinner-box with view onto a hologram stimulus (from a pigeon's perspective); c) Interior of the MSB: a real Greeble figure (mounted onto a slot of the rear wheel) is positioned behind the viewing tunnel; d) Interior of the MSB: a hologram plate (mounted onto a slot of the front wheel) is positioned behind the viewing tunnel.

Stimuli

We used two real 3D figures ("Greebles") and holograms thereof as stimuli (Fig. 2a). Greebles are "face-like" nonsense objects of homogeneous surface with protruding parts organized on a vertically oriented central part (Gauthier & Tarr, 1997). Thus, although Greebles are artificially designed stimuli, they are comparable to natural objects in that they can (roughly) be decomposed into parts (like "heads", "trunks", and “arms”). The shapes of the two Greebles chosen for the present experiment were selected to provide maximum discriminability of the two figures. For example, the trunk of one figure was concave whereas that of the other figure was convex, and one figure had one protruding part on the “head” (“horn”), whereas the other had two. We are aware that such distinguishing features could be introduced only at the expense of equivalence (for example, different numbers of horns resulted in different numbers of mirror planes). However, we prioritized discriminability over equity as the present study was aimed not at taxing the limits of pigeons’ and humans' discrimination abilities in general, but at investigating the influence of presentation mode on their ability to discriminate between stimuli that were, by themselves, well distinguishable.

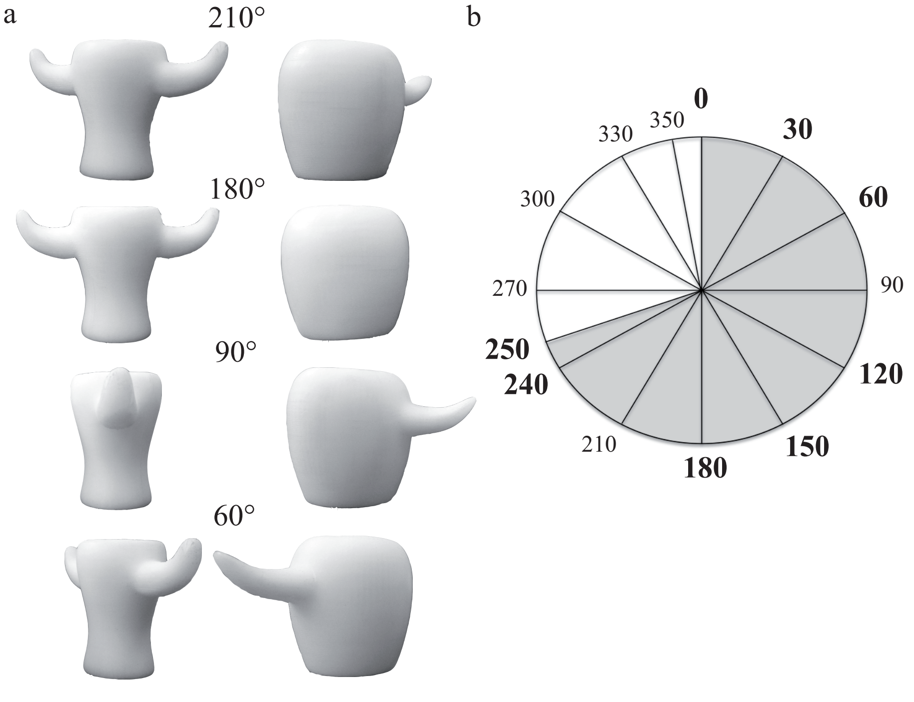

Figure 2 a) Examples of Greeble stimuli shown from different angles under daylight conditions. b) Schematic outline of the relationship between training views and test views. Gray area: training views (bold, large print) and novel interpolated views (small print); angles within the white area symbolize novel extrapolated views. All angles are measured relatively to an arbitrarily defined 0°-position.

Real objects

The real 3D Greebles were white plastic figures designed by CAD (computer aided design) software and produced by a milling machine. The motion of the machine (e.g. depth of cuts, speed or movement of the spindle) was controlled by a computer program (Computerized Numerical Control/CNC).

Holograms

The holograms we used were phase-modulation transmission holograms. With transmission holograms, the reconstruction beam is transmitted through the developed film, meaning that the source of illumination and the perceiving subject are located on opposite sides of the film. The holograms were recorded with an argon ion laser with a wavelength of 514 ± 1nm, which provided a sufficient coherence length (Fig. 3). The holographic material (*VRP-M*, by Slavich; see http://www.geola.com) was a silver halide film with a spectral sensitivity range of 413-570nm. It had an average grain size of 40nm and a resolution of at least 3000 lines/mm. The recording laser source was, however, too massive and not mobile enough to be integrated into the MSB~~.~~ Thus, for replaying the holograms, a green DPSS (Diode Pumped Solid State) laser with a wavelength of 532 ± 1nm was used instead. The laser source was also used for illumination of the real objects, thus providing light of the same quality (e.g. wavelength) in all presentation modes. The laser intensity was roughly adjusted with the laser device electronics. The laser light was then split into three beams: one for hologram replay and two for object illumination. Afterwards, the intensities of the beams were more accurately adjusted by means of neutral density filters and the laser beams were injected into optical fibres whose outlets were mounted in the appropriate positions for correctly illuminating objects and holograms. The wavelengths of both the recording and the replaying laser are known to match the spectral sensitivity maxima of pigeons (e.g. Emmerton & Remy, 1983; Campenhausen & Kirschfeld, 1998) as well as humans (e.g. Schnapf et al., 1987). As the real objects were shown in different orientations, it was necessary to generate several holograms of each Greeble, too, that showed it from different viewing angles. To this end, a 0°-view was arbitrarily defined, and holograms were recorded that differed from that orientation by 0°, 30°, 60°, 120°, 150°, 180°, 240° and 250° (see Fig. 2b). These were the same viewing angles as the ones under which the real objects were shown.

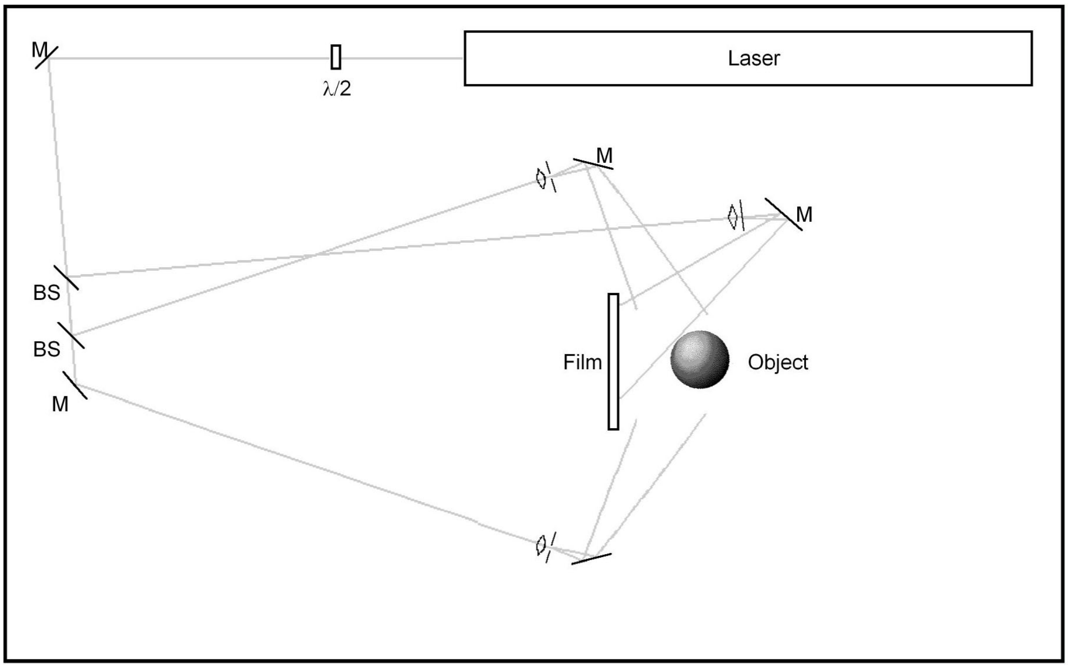

Figure 3 Schematic overview of hologram recording, as done to create the holograms for the present experiment. M = mirror; BS = beam splitter, λ/2 = retardation plate.

Procedure

The pigeons were trained and tested in a standard go/no-go procedure (e.g. Vaughan & Greene, 1984; Aust & Huber, 2001, 2006a, b). Positive trials required them to peck the response key in order to get food, whereas negative trials required them to refrain from pecking in order to avoid a delay. All birds were trained to discriminate between the two Greebles figures on a minimum of five days per week. Stimuli were presented in pseudo-random sequences, that is, no more than three positive or negative training stimuli (and, in the subsequent test phase, no more than one test stimulus) were presented in a row, and the first and the last stimulus of a session were always positive ones. Reinforcement contingencies of the two Greebles were counterbalanced across subjects, that is, one particular Greeble was positive for half of the birds of each group and negative for the others (and vice versa for the second Greeble).

A trial started with the presentation of the stimulus and pecks that were emitted between the 5th and the 15th second following the onset of stimulus presentation entered analysis (counting phase). Afterwards, the stimulus remained visible for another 0 to 15 seconds (variable interval), thus excluding any learning of temporal patterns during trials. A decision phase followed in which 2 pecks had to be emitted within 2 seconds in the presence of a positive stimulus before food was delivered. In order to encourage high response rates on positive trials, a minimum of 10 pecks in total was, however, required. This means that, should the pigeons, for example not have pecked at all until the onset of the decision phase of a positive trial, they had to emit 10 pecks then (not just two). On negative trials, pecking had to be inhibited for 8 seconds during the decision phase. Otherwise, stimulus presentation was prolonged for another 8 seconds. Hence, stimulus presentation lasted for a minimum of 17 seconds in positive trials (counting phase 15 seconds, plus variable interval 0 seconds, plus decision phase 2 seconds) and 23 in negative trials (counting phase 15 seconds, plus variable interval 0 seconds, plus decision phase 8 seconds). The actual duration of a trial depended on the duration of the variable interval (which could last up to 15 seconds) as well as on how quickly the pigeons fulfilled the response requirement. Meeting the response requirement in the decision phase (i.e.

pecking on positive trials and not pecking on negative ones) resulted in 5 seconds of food access on positive trials and termination of negative trials. Food was never provided on negative trials. There was no decision phase on test trials, but they were terminated after 15 seconds and resulted neither in food access nor in a delay, independently of the subject's response behaviour. Each training and test trial was followed by an intertrial interval (ITI), a dark phase that signalled the forthcoming of the next stimulus. Due to mechanical constraints inherent in the apparatus but also in order to avoid any influences of temporal patterns, the ITI ranged from 15 to 40 seconds.

For humans, the procedure was the same as for the pigeons, apart from some minor adjustments, e.g., regarding the operant chamber and the control device (see also apparatus section). Human participants were not rewarded on positive trials, that is, the only feedback they got was the disappearance of the stimulus at the end of the decision phase. Prior to the experiment, participants were told that they were about to take part in a human-pigeon comparison study on visual cognitive abilities. They were informed about the basic logic of the procedure and were asked to press a button at an estimated frequency of at least 2 per second in response to stimuli they assumed to be positive. Furthermore, they were told to indicate their level of certainty regarding stimulus contingency in each trial by producing graded clicking rates and were asked to start responding as soon as the stimulus appeared. Human participants were trained and tested two to three times a week in sessions of 1 to 1.5 hours. In sum, the experiment lasted for approximately 10 hours for humans.

Discrimination training

The training procedure was the same for pigeons and humans with the exception that the learning criterion was more lenient for humans in order to keep the experiment as short as possible and due to highly reliable discrimination performance already at very early stages of training (see data analysis). Training sessions consisted of 32 trials, 16 positive and 16 negative ones. The training stimuli were shown at viewing angles of 0°, 30°, 60°, 120°, 150°, 180°, 240° and 250 ° relative to an arbitrarily defined 0°-orientation (see stimulus section and Fig. 2b). Four different viewing angles for each of the two Greebles (i.e., eight different stimuli in total) were shown in a session, with each stimulus being presented four times. Due to restrictions in the number of stimuli that could be attached to a wheel (i.e., 8; see apparatus section), each session involved viewing angles of either 0°, 30°, 60° and 120°, or 150°, 180°, 240° and 250°, with the 0°-120° and the 150°-250° sets being shown on alternating sessions. When the subjects performed at criteria level (see data analysis section), they were transferred to the Hologram-Object Equivalence test.

Hologram-Object Equivalence test

In order to test for transfer of the training discrimination to the other presentation mode, humans and pigeons were presented on test trials with Greebles stimuli under the same viewing angles as shown during training (0°, 30°, 60°, 120° 150°, 180°, 240°, 250°), displayed as holographic images for Group Object and as objects for Group Hologram. That is, a total of 16 test stimuli were shown (i.e., eight for each Greeble). All subjects were presented with each test stimulus six times, resulting in 96 test trials overall. Pigeons were administered 30 trials per session — 24 training trials and 6 randomly interspersed test trials. The test procedure was the same for humans except that the number of training trials per session was reduced to twelve in the service of conciseness. Thus, each test session consisted of 18 trials in total.

Data analysis

Assessments of training performances were based on rho *(ρ)*-values, a non-parametric measure derived from the Mann-Whitney U-statistic (Herrnstein et al.,1976). For pigeons, the critical ρ-value to indicate significance in training sessions ($_1N_2 = 16$) was 0.697, and the learning criterion was defined as significant discrimination in 4 out of 5 consecutive sessions. For the assessment of test performances ($_1N_2=6$) the critical ρ-value was 0.813.

Differences in the number of training sessions needed by pigeons of Groups Object and Hologram to reach criterion were assessed by means of a Mann-Whitney U test, and so were differences in discrimination performance between groups or reinforcement contingencies. As all human participants reached ρ-values of 1.000 (indicating perfect discrimination) within the first session of training, their acquisition phase was reduced to two consecutive sessions.

Evaluation of individual test performances was based on mean standardized response rates, calculated by dividing the total number of pecks emitted on a particular trial (training or test) by the average number of pecks emitted on training trials in that session. Performance was then assessed by comparing mean standardized response rates emitted to the positive and the negative Greeble on test trials by means of Mann-Whitney U tests. Differences in the test performances of the two groups were assessed by comparing ρ-values obtained by the six subjects of each group on the test stimuli by means of Mann-Whitney U tests. Similarly, training and test performance within groups was assessed by comparing the ρ-values obtained by the six subjects on training and test stimuli by means of Mann-Whitney U tests. All statistical analysis was conducted using SPSS v. 17.

RESULTS

Discrimination training

For pigeons, there was no effect of training contingencies on the accuracy of discrimination in either group, calculated across all viewing angles and with ρ-values being pooled for each group. That is, it did not "matter" which Greeble was the positive and which was the negative one. Pigeons of Group Object learned faster and thus needed fewer sessions to acquire the criterion of mastery (8 on average) than subjects of Group Hologram (19 on average), and this difference was statistically significant ($P \leq 0.01$). Human participants of both groups showed perfect discrimination already in the first training session ($\rho = 1.000$) and maintained their excellent performance in the second one.

Once the pigeons had acquired reliable and consistent discrimination, birds of Group Object emitted a median of 19.5 pecks to positive stimuli (range: 8-39) and a median of 5 pecks to negative stimuli (range: 0-32). This was comparable to the performance of the birds in Group Hologram who emitted a median of 25 pecks to positive stimuli (range: 0-36) and 6 to negative stimuli (range: 0-31). Human participants in Group Object made 28 clicks (median) to positive stimuli (range: 0-46) and 0 clicks to negative stimuli (range: 0-32). Group Hologram made 34 clicks (median) to positive stimuli (range: 22-46) and 0 (median) clicks to negative stimuli (Fig. 4).

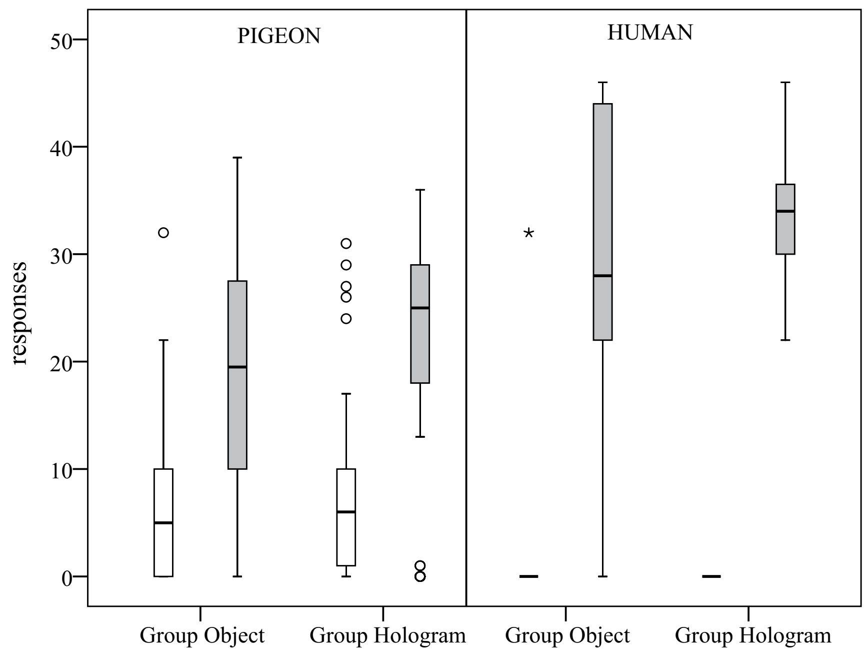

Figure 4 Response behaviour of pigeons and humans at the end of discrimination training. White boxes represent the number of pecks (pigeons) or clicks (humans) to negative stimuli, grey boxes represent the number of responses to positive stimuli. Each box indicates the first (bottom of each box), the third (top of each box) and the median (horizontal line) of the number of responses. Whiskers include values that amount to 1.5 times the height of the box. Circles indicate outliers that do not fall in the inner fences (whiskers) whereas asterisks indicate extreme outliers, representing values more than three times the height of the box.

Hologram-object Equivalence

The comparison of mean standardized response rates for individual pigeons showed that all subjects were able to transfer the training discrimination to the other presentation mode with all viewing angles (Mann-Whitney U tests; for all individuals: $P \leq 0.0001$). As during training, contingency had no effect on performance, neither in Group Object, nor in Group Hologram.

Pigeons of Group Hologram showed equally good discrimination on training and test trials (Fig. 5b). Subjects of Group Object, however, performed significantly better with test stimuli (i.e., holograms) than with training stimuli (i.e., objects; $P \leq 0.05$, Fig. 5a). Furthermore, test performance of Group Object was better than that of Group Hologram ($P \leq 0.01$). That is, Group Object transferred the discrimination more accurately to holograms than did Group Hologram to objects.

Like the pigeons, all human participants could well generalize to the other mode of presentation with all viewing angles (for all individuals: $P \leq 0.0001$). Both Group Object and Group Hologram performed equally well on test and on training trials, but transfer was better in Group Hologram than in Group Object ($P \leq 0.01$; Fig. 5c, d). However, detailed analysis revealed that inferior performance of Group Object was mainly due to somewhat less reliable discrimination displayed by one single individual. Responding behaviour of the same individual gave rise to an effect of training contingency that was revealed in humans of Group Object ($P \leq 0.01$). No such effect was found in Group Hologram.

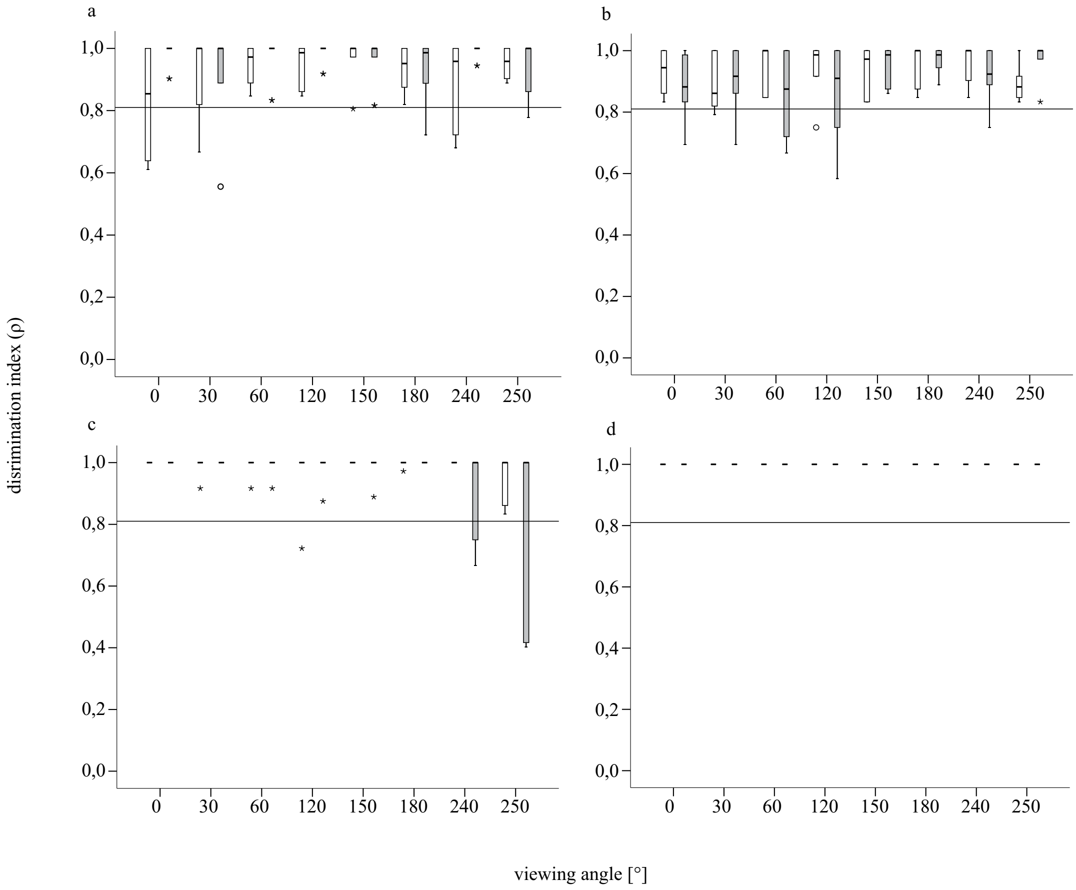

Figure 5 Training performance (white boxes) and transfer to the presentation mode not experienced during training (grey boxes). The box plots show the distribution of ρ-values separately for the various viewing angles, for a) pigeons of Group Object, b) pigeons of Group Hologram, c) humans of Group Object and d) humans of Group Hologram. The horizontal line indicates the limit of significance ($\rho = 0.813$). The bottom of each the box indicates the first, the top indicates the third quartile. The horizontal line within each box represents the median. Whiskers include values that amount to 1.5 times the height of the box. Circles indicate outliers that do not fall in the inner fences (whiskers). Asterisks indicate extreme outliers and represent values more than three times the height of the box.

DISCUSSION

Discrimination training

Pigeons of Group Object acquired the learning criterion significantly faster than those of Group Hologram. The fact that the presentation of real objects obviously facilitated discrimination compared to holograms (or that the presentation of holograms impeded discrimination) is interesting as, from a physical point of view, the two presentation modes should be equivalent. For now, we may only speculate on possible reasons for the observed inter-group difference, but, most likely, it has to be attributed to some methodological artifacts. For example, holographic images had to be viewed through a glass plate (i.e., the carrier of the holographic film), which could have confused the birds. In particular, it is possible that they focused on the closer plane of the glass plate (attached to the front wheel at a viewing distance of about 11cm) and may not have realized that the actual stimulus they were supposed to attend to was the holographic image farther behind (presented at a viewing distance of about 26cm). If so, the prolonged training of Group Hologram relative to Group Object may reflect the difficulty the former encountered giving up their initial preference for the plane of the glass plate and directing their attention to the projections behind. Considering that pigeons are assumed to preferentially use their frontal visual field for myopic foraging (while their lateral fields have been claimed to be specialized for more global, wide field perception in the service of predator detection and flight control; see Cook, 2001), such an explanation may indeed be plausible. Importantly, Cook (2001) reported declines in pigeons' accuracy of stimulus location with increasing viewing distance. Thus, if the pigeons attempted to use their frontal rather than their lateral field in the present experiment (just like they presumably do in natural feeding contexts), this may initially have biased them towards focussing on the closer plane of the glass plate rather than on the holographic images farther away. Obviously, they eventually learned to ignore the glass plate and to focus on the holograms behind in the course of training, but this need to give up their initial preference and to re-focus their attention may have put them at a disadvantage compared to Group Object, which was trained without any potentially distracting glass plate. Perfect performance of both groups from the very first session onwards showed that, other than the pigeons, the human participants were not influenced by any such effects.

Further experiments entailing some modifications in the apparatus and stimulus material will thus be needed to pinpoint and eliminate possible methodological artefacts that may have led to the observed differences between Groups Hologram and Object in pigeons. A simple but critical measure will, for example, be the use of a (functionless) glass plate inserted into the hologram wheel also during the presentation of objects. Should the presence of a glass plate indeed have impeded learning in Group Hologram in the present study, the same difficulties should then be faced also by Group Object and acquisition performance should no longer differ between the two groups.

Hologram-Object Equivalence test

All subjects, humans and pigeons, showed excellent transfer of the discrimination learned during training to the other mode of presentation, which is evidence that they perceived and thus treated both types of representation — real objects and holograms — as similar or even equivalent. Interestingly, however, pigeons of Group Object performed even more accurately with holograms than with real objects (whereas Group Hologram performed equally well with objects and holograms). Considering the difficulties the birds of Group Hologram had in acquiring the training task with holographic images, this “hologram superiority effect” observed in Group Object is difficult to interpret in a straightforward manner. It is, for example, conceivable (though speculative) that Group Object was at an advantage because (in the absence of the glass plate) they had learned to focus on the "correct" plane right from the beginning of training and thus ignored the glass plate on test. In addition, some general difference in quality between object and hologram presentation may have played a role. It is, for example, possible that some discriminative features (related, e.g., to stimulus shape or overall size) were more salient in holograms than in objects, for instance as a consequence of slight differences in illumination intensity between the two presentation modes. Although we controlled for illumination differences to the greatest possible extent, they may not have been removed completely and may have led to a non-linear enhancement of the observed advantage of holographic presentation – particularly if they affected intensities to which pigeons are highly sensitive (e.g. Biederman et al., 1988; Wixted & Gaitan, 2004). This may explain why performance of Group Object was not just equally good with holograms as with objects, but even better.

Group Hologram had obviously overcome their (assumed) preference for focusing on the plane of the glass plate by the onset of the first test and showed excellent discrimination with both training and test trials. Critics may wonder, however, why they did not perform somewhat worse on the test stimuli (objects) than on the training stimuli (holograms), provided that the latter were indeed easier to discriminate (e.g., due to enhanced illumination differences). One possible explanation is that Group Hologram focussed on other discriminative features than did Group Object, namely ones that did not enhance discriminability of holograms relative to objects.

The human participants performed equally well in training and test trials. Furthermore, no difference in transfer performance was found between Groups Object and Hologram. This may either indicate that the humans used different features for discriminating between the two Greebles figures than did the pigeons or that they were not so sensitive to subtle differences between object and hologram presentation as were pigeons. Nonetheless, one human subject of Group Object was obviously influenced by the particular contingencies of reinforcement (i.e., S+ or S-) associated with each Greeble. This may reflect a feature-positive effect in that individual (Pace et al., 1980; Nallan et al., 1983; Lindenblatt & Delius, 1988; Aust & Huber, 2001), and/or be indicative of inter-individual differences in discrimination strategies. Further experiments with larger sample sizes will be needed to clarify this issue.

Experiment 2: Rotational invariance

INTRODUCTION

The second experiment investigated the suitability of holograms as stimuli to address one of the most important visual abilities of highly mobile species, namely rotational invariance. In a dynamic world, mobile organisms like pigeons and humans constantly have to integrate visual information of objects across various viewing angles. Consequently, rotational invariance is essential for object recognition independently of position and orientation (Hollard & Delius, 1982). Humans are known to recognize objects even from viewing angles they have not experienced before (Shepard & Metzler, 1972; Biederman & Gerhardstein, 1993), although results are not completely consistent. The mechanisms that underlie the recognition of novel object views may be explained by two alternative approaches. The viewpoint-independent approach suggests recognition of novel object views on the basis of structural information, namely components and their configuration (Biederman, 1987; Hummel & Biederman, 1992). The other approach is less object-centered and proposes a viewpoint-dependent recognition mechanism that is based on the perceiver. According to this account, object recognition emerges from the comparison of novel with stored familiar object views (Tarr & Pinker, 1990; Tarr & Bülthoff, 1995; Tarr et al., 1997). Thus, viewpoint-independent approaches predict that object recognition will become more difficult if crucial object components are not visible in novel views whereas viewpoint-dependent approaches predict less reliable recognition of objects with farther rotations from known orientations. Studies with pigeons have yielded inconsistent results. Rotations in the picture plane were found to have no detrimental effect on pigeons' performance whereas rotations in the depth plane led to significant performance decrements (Cerella, 1990; Peissig et al., 2000). Generally, whether or not both pigeons and humans are able to integrate various viewpoints of an object into a unified object description seems to depend crucially on whether novel views lie within the range of familiar viewing angles (interpolated views) or beyond (extrapolated views). Spetch and her collaborators (2001) found poorer performance with farther than with closer distances from training views and better performance with interpolated than with extrapolated novel views in humans. In pigeons, recognition accuracy was found to decline with farther rotations from training views (Spetch & Friedman, 2003). The present experiment contributes to the current discussion surrounding the question of rotational invariance by investigating transfer to previously unseen views of real objects and holograms. To this end, pigeons and humans were presented in a follow-up experiment with novel (interpolated and extrapolated) views of the two objects (Group Object) or holograms (Group Hologram) they had been trained to discriminate in Experiment 1.

METHOD

Subjects, apparatus, and procedure

We used the same subjects as in Experiment 1, which were tested with the same apparatus and with the same general procedure as used in Experiment 1. Pigeons and humans were presented with novel views of stimuli in the same presentation mode as experienced during training (i.e., Group Object was tested with novel views of objects; Group Hologram was tested with novel views of holograms). Prior to testing, the maintenance of reliable and consistent discrimination of training stimuli was ensured in all subjects by giving them 4 additional training sessions and checking if they still performed at criteria level. As this was the case for all birds, they could be transferred to the test without any further retraining.

Stimuli

Test stimuli were of two different types, namely interpolated and extrapolated views, depending on whether their angle of rotation lay within (interpolated: 90°, 210°) or beyond (extrapolated: 270°, 300°, 330°, 350°) the training range (Fig. 1b). Thus, 12 different test stimuli were shown (6 views of each Greeble) and all subjects were presented with each test stimulus six times overall, resulting in a total of 72 test stimuli. In each test session, one novel test view of each Greeble was presented three times. Thus, the entire test consisted of 12 sessions. The pigeons were given sessions consisting of 24 training and 6 test trials, amounting to a total number of 30 trials per session. For humans, test sessions consisted of 18 trials — 12 training and 6 test trials.

Data analysis

The comparison of group performances in discriminating test stimuli and comparisons of training and test performance within groups followed the same general protocol as in Experiment 1. For a more detailed analysis, we additionally pooled performances of all subjects on a particular viewing angle within a group and compared the performance to positive and negative stimuli in each viewing angle on a group level by means of Mann-Whitney U tests.

Table 1 Transfer to novel viewing angles in the Rotational Invariance test. Mean standardized response rates emitted to positive and negative test stimuli by all individuals of a group were compared by means of Mann-Whitney U tests and are displayed at group level. Significant *p*-values are indicated by bold typeface.

		Novel views					
		interpolated		extrapolated			
		90°	210°	270°	300°	330°	350°
Pigeons	Group Object	**≤0.0001**	**≤0.0001**	**≤0.05**	n.s.	n.s.	n.s.
	Group Hologram	**≤0.0001**	**≤0.0001**	**≤0.01**	n.s.	**≤0.05**	n.s.
Humans	Group Object	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**
	Group Hologram	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**	**≤0.0001**

RESULTS

Pigeons of both groups had more difficulties discriminating novel extrapolated than novel interpolated views (Table 1). Indeed, the comparison of mean standardized response rates emitted to positive and negative test stimuli of each view revealed that Group Object showed transfer only to one out of four novel extrapolated views, whereas the birds consistently performed at a highly significant level with novel interpolated views. A similar pattern was apparent in Group Hologram. Accordingly, both groups showed significant performance decrements for extrapolated novel views relative to training views (Group Object: $P \leq 0.001$; Group Hologram: $P \leq 0.001$, Fig. 6a). With novel interpolated views, by contrast, performance was as good as on training trials in both groups (Fig. 6a). No differences in performance were revealed between Groups Object and Hologram, neither for interpolated nor for extrapolated novel views (Fig. 7). Furthermore, there was no effect of training contingencies in either group.

Unlike the pigeons, both groups of humans showed good transfer not only to the interpolated novel views, but also to the extrapolated ones (Table 1, Fig. 6b). Neither human group showed any difference in performance with novel interpolated or extrapolated views, relative to performance on training trials. As with the pigeons, there were no differences between the performances of the two groups, neither for interpolated nor for extrapolated novel views. However, as in the Hologram-Object Equivalence test, the ρ-values obtained by Group Object indicated some differences in the accuracy of discrimination depending on training contingency ($P \leq 0.05$). This bias was found to be due to the responding behaviour of the same individual as in the previous test. Interestingly, this subject of Group Object showed less reliable discrimination than the others for one interpolated test view (90°) and all extrapolated test views (reflected by increased click rates to negative stimuli and decreased click rates to positive stimuli). No such effect was seen in Group Hologram.

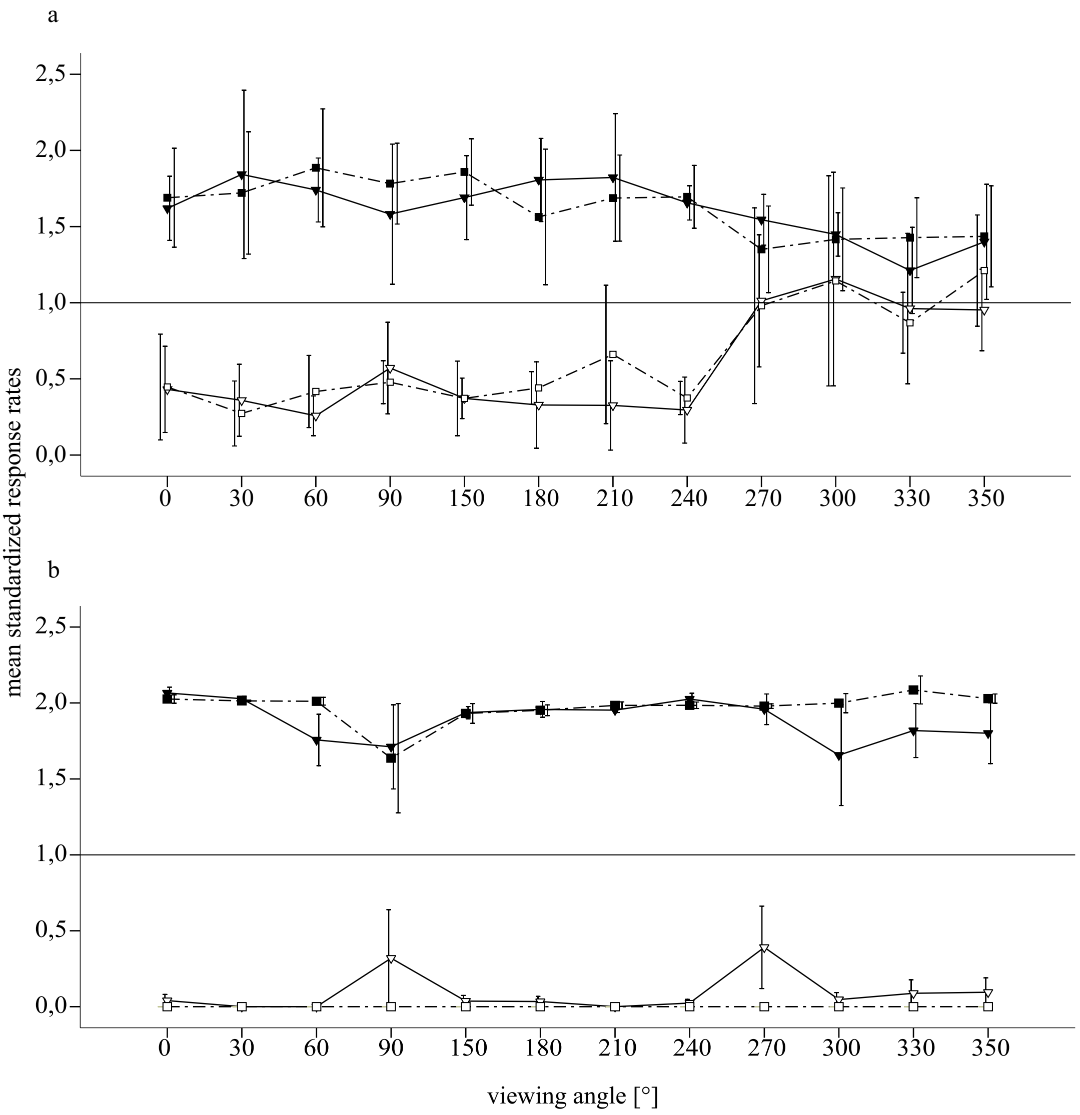

Figure 6 Results of the Rotational Invariance test obtained for all viewing angles, shown separately for both groups of pigeons (a) and humans (b), as mean standardized response rates (± SD) that were emitted to positive (black symbols) and negative stimuli (white symbols). Squares represent performance in Group Hologram (pigeons and humans), triangles represent performance in Group Object (pigeons and humans). The horizontal line marks the level of chance performance.

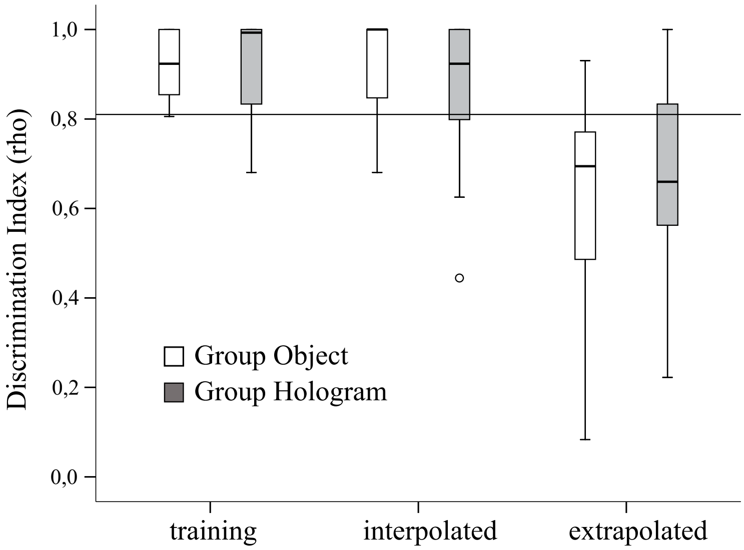

Figure 7 Discrimination performance of pigeons with novel interpolated and extrapolated views in the Rotational Invariance test, shown as ρ-values. The bottom of the box indicates the first, the top of the box the third quartile. The horizontal line within the box represents the median. Whiskers include values that amount to 1.5 times the height of the box. Circles indicate outliers that do not fall in the inner fences (whiskers). The horizontal line marks the limit of significance ($\rho = 0.813$).

DISCUSSION

Pigeons of both groups successfully transferred the discrimination learned during training to novel interpolated views with performance on training and test trials being equally good, whereas the presentation of extrapolated views resulted in significant performance decrements. The lack of any performance differences between Groups Object and Hologram suggests that the mode of presentation during training had no impact on the pigeons’ ability to transfer to novel views.

All humans except one successfully transferred to novel views, with neither the type of test stimuli (interpolated or extrapolated) nor the mode of presentation during training (real objects or holograms) affecting performance. Again, one subject of Group Object was either influenced by a feature-positive effect or performed differently from the others due to individual preferences regarding response strategies.

The present results confirm those of Friedman et al. (2005) who found that pigeons performed more accurately with interpolated than with extrapolated novel views when test views differed from training views by only 30°. Furthermore, several studies reported that pigeons benefitted from multiple training views, and that generalization gradients were flattest when distances between training views were large (Kirkpatrick, 2001; Peissig et al., 2002). We tried to take both findings into account by using eight different training views, with neighbouring views differing by 36° on average and, indeed, found significant decrements in performance with extrapolated novel views, as reported by Friedman et al. (2005).

Regarding humans, our results did not match those previously reported by Spetch and Friedman (2003). While they found humans to show decreased discrimination accuracy for extrapolated novel views of structurally complex stimuli, humans in the present study did not show any effect of the degree of rotation from training views on the discrimination of novel views. However, as the present experiment used stimuli that were very different from the ones employed by Spetch and Friedman (2003), the two studies cannot be compared in any straightforward manner regarding the structural complexity of stimuli and its possible impact on the discrimination of interpolated and extrapolated novel views. Moreover, Spetch and Friedman (2003) used only two different training views whereas eight were used in the present experiment, and we suspect that this higher number of training views had an additional facilitating effect on humans' generalization to novel views, independently of their distance from training views (Cook et al., 1990; Logothetis et al., 1994).

In summary, two main findings emerged from the Rotational Invariance test. First, the results are evidence of pigeons and humans being able to transfer the discrimination between two stimuli to previously unseen viewpoints when presented either as real objects or as holograms. Of particular importance is the finding that the results obtained with holograms were, for the most part, in keeping with those of earlier studies that used more traditional types of stimulus types like real objects or movies. This is further evidence that holograms may, indeed, make suitable stimuli for visual discrimination experiments. Second, the fact that pigeons' performance dropped dramatically with novel views that lay beyond the training range whereas humans performed equally well with all novel views points to some inter-specific difference in rotational invariance. Additional experiments will be needed to clarify whether, apart from this, pigeons and humans applied similar strategies (e.g. used the same features) for solving the task.

GENERAL DISCUSSION

The results reported here represent, to the best of our knowledge, the first attempt ever to employ holographic stimuli in a visual discrimination task. As it stands, holograms are the closest to the visualization of a real object that can be achieved, providing exactly the same physical information as objects do when illuminated in the same way. By combining the advantages of real objects and 2D-pictures while avoiding some of their most troublesome disadvantages, this technology provides a powerful tool for investigating the perceptual and cognitive abilities of animals and humans in a comparative way. Like real objects, holograms provide full 3D-shape information, thus bypassing a number of methodological problems encountered with photographs or computer images. Yet there are many possibilities to easily and flexibly modify the appearance of a holographic image.

The present experiments have taken an initial step into this yet unexplored direction by yielding preliminary baseline data collected with pigeons and humans and have thereby provided promising ground for future work with holograms. The finding that both species learned to discriminate between two objects in either presentation mode (real objects or holograms) and showed excellent transfer also to the previously untrained mode suggests perceived equivalence of both stimulus types. It has to be acknowledged that, for the pigeons, this conclusion can be drawn only with some reservations for now, considering the differences in acquisition speed and transfer performance of Groups Hologram and Object. But there is good reason to assume that these differences resulted from some methodological artefacts rather than from the perception of a genuine difference between the two stimulus types as such. We are aware that the present study may indeed have raised more questions than it answered, but it must not be forgotten that the combination of cognition research and holography is new territory. Consequently, the methods used in the experiments reported here may have been tainted with some "teething problems" that are, however, inevitable with any innovative approach. Future research will, above all, have to pinpoint the reason(s) for the performance differences between Groups Object and Hologram observed with the pigeons, and to eliminate the source(s) of these differences (e.g. the presence/absence of a potentially distracting glass plate, residual differences in illumination, etc.). Indeed, longer acquisition phases in Group Hologram compared to Group Object and different performances in the transfer to the other presentation mode showed that pigeons may be highly sensitive to subtle differences in the illumination regime or the spatial plane they focus on. Should further experiments with improved methodology confirm the suitability of holograms as stimuli, this would open up a wide range of research possibilities. In particular, holograms may be useful for investigating the importance of the 3rd dimension in various kinds of visual tasks. Amodal completion, for example, requires the perception of two layers (the one of the occluder and the one of the occluded object) and it is possible that pigeons' repeatedly reported failure in such tasks (Cerella, 1980; Sekuler et al., 1996; Watanabe & Furuya, 1997; Fujita, 2001a, 2001b; Ushitani et al., 2001; Fujita & Ushitani, 2005; Aust & Huber, 2006a) has been due to their inability to infer the 3rd dimension from two-dimensional stimuli rather than to lacking amodal completion abilities. It may thus be promising to re-investigate the issue with 3D rather than with 2D stimuli, with holograms possibly being a better choice than real objects, due to their higher versatility and manipulability. Similarly, holograms may be a powerful tool to investigate structure-from-motion. So far, video presentations have usually been used to investigate the inference of structural information from motion (e.g. Cook & Katz, 1999; Jitsumori & Makino, 2004; Loidolt et al., 2006;

Kramer, 2010) but, of course, these simulations did not provide “true” motion (i.e. smooth motion in depth). Holograms may serve to actually rotate stimuli in the depth plane and thus to eliminate any confounding effects of unrealistic stimulus presentation.

In short, a number of intriguing research questions that may be investigated with the help of holography are conceivable, and modern ways of hologram generation and presentation — like polychromatic or digital holography —, will certainly be the technologies to point the way ahead. Computer-generated holography (CGH), for instance, involves computation and generation of wave fronts and the corresponding interference patterns for holographic replay. The computed interference patterns are subsequently “printed” onto a holographic medium. Illumination by a suitable light source then produces the holographic image. Thus, stimulus generation and manipulation are neither dependent on the existence nor the availability of real objects and any modification could easily be replicated. Although the corresponding computations are quite complex, CPG will certainly play a major role in the future because a huge variety of 3D-stimuli would become available in experiments on visual cognition, comparable to those that are already standard with 2D-stimuli created by computer graphics. Together with their high resistance to external influences (like mechanical damage) this versatility may indeed make holograms superior to real objects as stimuli to be used in visual discrimination and categorization tasks.

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SUPPLEMENTARY MATERIAL

Basic facts about holography

In conventional photography the intensity (i.e., the square of the amplitude) of the light hitting the film is recorded on the film. In color photography information about the wavelengths/frequencies is recorded (i.e., “red”, “green” and “blue”) in different film layers. In replaying mode (after development of the film) these layers produce the respective complementary colors (cyan, magenta and yellow). The light as it comes from real objects is not only specified by its amplitude and wavelength/frequency but also by its phasing. This latter information is lost in photographs, and with it directional information and thus the 3D-effect. Holography is a technique that allows for recording and retrieving not only the intensity of the incident light, but also its phase and thus directional information, i.e., the *complete physical information*. This is accomplished by a recording being captured as an interference pattern at the film.

The basic techniques of holography were introduced by the 1971 Nobel prize laureate Dénes Gábor and by Emmeth Leith and Juris Upatnieks (Gabor, 1948; Leith & Upatnieks, 1962; Saxby, 2004). A monochromatic light source (a very tiny bandwidth of wavelengths/frequencies) produces a highly coherent light beam, i.e., the light beam’s constituents (photons, or their wavefields, respectively) are synchronous in phase over a wide length (the coherence length is a measure for this). The light is split into two beams, the object beam and the reference beam. The object beam is scattered by the surface of the object to be recorded and the light reflected by the surface then interferes with the non - scattered reference beam. The resulting interference pattern is recorded with traditional photographic methods (although photographic films do not meet the quality requirements of holography). The phase difference between object and reference waves is stored in the recorded interference pattern (which is the reason why highly coherent light is required). The recorded interference pattern is called the *hologram*. When the hologram is afterwards appropriately illuminated during replay it replicates the light that originally came from the recorded scene (the object wave). It can be viewed from any distance and any orientation like the original object. In other words, the wavefront perceived by the viewer is indistinguishable from the wave front the object had scattered onto the recording film. Thus, the light coming from a hologram is identical to the light coming from the corresponding "real" object (see Fig. A1).

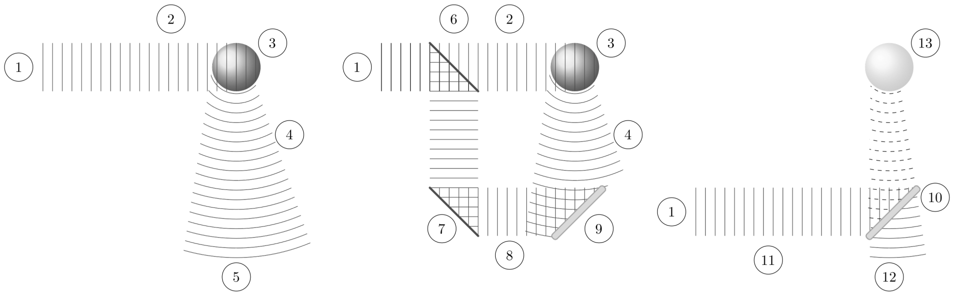

Figure A1 The principle of holography. Left panel: An illuminated object as seen by the observer. Middle panel: Basic procedure of hologram recording. Right panel: Replay and virtual image. (1) Coherent light source (laser), (2) illumination beam, (3) real object, (4) object beam, (5) wave front perceived by the observer, (6) beam splitter, (7) mirror, (8) reference beam, (9) holographic film, (10) hologram (developed film), (11) reconstruction beam, (12) reconstructed wave fronts, (13) virtual image.

There are several types of holograms, with the basic distinction being that between transmission and reflection holograms. They differ regarding the reconstruction of the recorded wave field, which is accomplished by the transmission of light through the developed film in the former, and by the reflection of light from the surface of the developed film in the latter. In addition, thin film holograms, in which the holographic film is thinner than the width of the interference pattern spacing, have to be distinguished from volume (or thick) holograms, in which the film's thickness is equal to or exceeds the width of the interference spacing. Thick films therefore allow for recording changes of the interference pattern also in the depth dimension, whereas thin films allow for the generation of surface holograms only.

Reconstruction of the wave field can be accomplished by either amplitude or phase modulation. In the case of amplitude modulation the interference pattern is recorded by means of modulations of the optical permeability of the developed film. In the case of phase modulation the interference pattern is recorded by means of modulations of either the film's thickness or its refractive index. During replay the phase of the transmitted light is then shifted when passing the holographic medium so that the resulting wave field matches the original one (i.e., that of the recorded object). Generally, phase holograms are more efficient than amplitude holograms because the amount of light that passes through (which depends on optical permeability) is much higher in the former (for a more comprehensive introduction into the basics of holography see, e.g. Collier, Burckhardt, & Lin, 1971; Saxby, 2004; Ackerman & Eichler, 2007).

Holograms as stimuli

In principle, holographic presentations allow for real 3D - viewing, i.e., parallax and depth viewing from various different angles. However, realized viewing angles under which the holographic image can be seen depend on the particular mode of recording and reproduction of holograms. This effect is illustrated in Fig. A1: the original object wave front perceived by the observer (5) and the holographic reconstruction thereof (12) show different opening angles. Observers located within the respective opening angle of the reproduced wave front cannot distinguish the virtual image from the real object. Leaving the appropriate solid angle, however, inevitably leads to distortions of the perceived image. Circulation around the virtual object as well as 360 °-rotation of the latter is not possible. To bypass the limitation of possible positions of the observer one could employ so-called 360° - holograms. With these, a toroidal holographic film encloses the object and the reference beam as well as the reconstruction beam enter from above or beneath the object thus allowing viewing from all directions in the horizontal plane. By rotating the film during replay, this technique allows for the presentation of rotating holograms. Hence the observer perceives a rotating virtual image of the object, including information from all viewing angles without, however, changing the observers's own position.

So far, holograms have not been used in animal cognition research, despite the advantages they provide. Like real objects, holograms provide full 3D shape information and may thus be a powerful means for investigating to what extent the 3rd dimension supports recognition and categorization. Compared to real objects holograms bear the advantage of offering many possibilities of systematically modifying the appearance of a stimulus. It can be gradually modified in many different ways and the question can be addressed which types and which degrees of modification will deteriorate performance to what extent. For example, replay wavelength, size, or viewing angle can be manipulated. Also, holograms varying with respect to spatial frequencies are conceivable. This latter type of modification would, however, require digital holography:

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CHAPTER 6: CONCLUSION

The empirical data presented in this thesis amend our knowledge about some less well-known traits in pigeons' ability to abstract a common function from different external entities. Specifically, pigeons were shown to integrate information that was perceived in different sensory modes, to possess a remarkable behavioural flexibility depending on contextual information and to transfer an individually learned consequence of encounters with real-life entities to pictures thereof. Furthermore, although two studies presented here suggest successful picture-object recognition, the vast majority of studies in visual discrimination task would benefit from stimulus presentation techniques that are not bound to pictorial presentations. Some of the experiments reported here addressed this need by using a novel method that employs holograms as stimuli and that provides a promising approach not only for the investigation of functional class formation.

Pigeons were previously shown to possess extraordinary memory capacities (Vaughan & Greene, 1984; Cook et al., 2005), which seem to be similar in kind to those of non-human primates with respect to how both species store and assess a large amount of stimulus-response associations. Nonetheless, monkeys usually outcompete pigeons in the number of memorized items (Fagot & Cook, 2006). However, the memorization of stimuli often seemed to be based on associative learning of stimulus and reward and only few studies showed the birds' ability to refer to the actual function or the referential content of stimuli (e.g. Aust & Huber, 2006; Dittrich et al., 2010; Wilkinson et al., 2010; Belguermi et al., 2011). During visual discrimination tasks, pigeons were previously shown to possess a certain flexibility with regard to the strategy they use to accomplish successful categorization by switching between different levels of perceptual information (Aust & Huber, 2001, 2003; Cook, 2001).

Whether pigeons are also able to infer information context-dependently and to flexibly adjust complex behavioural responses remained unknown. In particular, flexibly responding to physically identical signals would require the birds not only to decode the function and consequence of the information itself but also to take the context into account in which this piece of information is perceived. So far, these highly sophisticated inferring skills have mainly been shown in non-human primates (e.g. Zuberbühler et al., 1999; Snowdon, 2009) and in some species of the corvid family (e.g. Bugnyar & Heinrich, 2006). As a consequence, the level of sophistication in cognitive abilities of bird species has been thought to be mainly genetically predisposed (Emery, 2006).

In contrast to these previous results, the predation avoidance experiment presented in Chapter 2 not only gives evidence for pigeons' ability to spontaneously recognize a predator, but also for the integration of acoustic and visual information and for the ability to take contextual information into account. The term "spontaneously" here refers to the absence of an experimental acquisition phase in which the birds learned the discrimination and does not imply that they did not learn about the consequences of predator presence during their ontogeny. Apparently, pigeons judged the novelty of information by comparing previous knowledge with present information, independently of the perceptual dissimilarity of stimuli (due to different modalities). The birds showed a remarkable behavioural flexibility in their responses to predator cues depending on previously acquired information and the sensory mode in which these cues were perceived. The results indicate that pigeons perceived buzzard-related stimuli as sharing a common consequence and thus as belonging to the same class ("predator"). Critically, correct classification could not be explained by mechanisms of generalization, as predatory cues were physically very different. Additionally, buzzard calls and buzzard models also seemed to represent different classes, defined by the level of urgency that was encoded. Pigeons formed a functional class of "predator" and within that class, additional subclasses that specified the urgency of the threat. These abilities are comparable to advanced inferring abilities that were previously found in some other mammal species (e.g. in meerkats and ground squirrels: Warkentin et al., 2001; Manser et al., 2002; Furrer & Manser, 2009). Whether buzzard calls and buzzard models also elicited mental representations of a flying raptor that hunts in a particular way, transcending the direct association between signal and response behaviour and including far more associations than those encountered in specific situations (as defined for humans, Hinde, 1974), cannot be concluded firmly from the present results. The formation of functional classes and the reference to contextual information are sufficient to explain observed behavioural responses. The stimuli used here resembled members of natural classes and the cognitive limits in the formation of functional classes may be best investigated with stimuli that are likely to be relevant in the birds' natural environment and whose recognition is supposed to have had a direct impact on the evolution of pigeons' discriminative abilities (Huber, 2000). The fact that all pairs of pigeons that received the same habituation/dishabituation stimuli performed consistently supports the relevance of predatory cues. These findings also further emphasize the necessity to use multi-modal signals to gain novel insights into pigeons' cognitive traits (e.g. Watanabe & Masuda, 2010) and highlight the cognitive disparity between signallers and receivers in animal communication (Fitch & Zuberbühler, in press). The investigation of categorization and referring abilities in more species with restricted vocal repertoires might provide a fruitful contribution to current debates about the transmission of information and intentional information sharing.

Pigeons were not only able to categorize predatory cues in their everyday environment but also to infer a class-binding abstract rule from pictorial presentation. As shown in Chapters 3 and 4, pigeons formed functional classes of inanimate objects and humans, which were based on previous real-life encounters (using the abstract discriminative feature of familiarity). Critically, the birds that lacked this kind of pre-experience were not able to acquire the discrimination, which renders it highly unlikely that conspicuous perceptual cues alone drove discrimination, although these may have added a facilitating effect on categorization (Aust & Huber, 2010a). The results support previous findings that proved pigeons to be able to refer to real-life experience during visual discrimination tasks (Aust & Huber, 2010b, Wilkinson et al., 2010). Hence, experience from real-life encounters could successfully be used to investigate the formation of functional classes by an abstract referent like familiarity but also to address picture-object correspondence in pigeons. Obviously, pigeons' perceptual and cognitive abilities have not co-evolved with the necessity to recognize man-made objects like green watering cans or protective helmets. Such objects have been only part of the birds' physical environment during the course of the experiments and were chosen to exclude differences between single objects regarding the length of pre-experience. Whereas advanced categorization and inferring abilities during predation avoidance are likely to have evolved during the species' phylogeny, the short-term flexibility in functional class formation with man-made objects is especially remarkable. Interestingly, the rapid memorization and categorization of objects seem to correspond to rapid learning and recognition of novel conspecifics after only 24h of direct contact (Wilkinson et al., 2010).

Most previous research on recognition based on familiarity focused on conspecific recognition (e.g. Van Dyk & Evans, 2007; Tricario et al., 2011) or on heterospecific recognition, providing further support for the notion that complex social systems (including heterospecific interaction) promote advanced cognitive abilities (e.g. Whiten & Byrne, 1997; Tibbetts & Dale, 2007). That pigeons in the present study successfully categorized also inanimate objects at least challenges the domain-specificity of advanced familiarity-based recognition. These short-term learning capacities may rather be due to the birds' ecology, namely the occupancy of very different habitats, often including rapidly changing urban areas that require the birds to adjust their behaviour in short time (Lee et al., 2011).

Pigeons' choice behaviour also seemed to be influenced by additional inherent functions of the objects. More specifically, the birds showed unlearned preferences for pictures of familiar objects that served an additional function in their everyday life, which is in keeping with previous findings that emphasized the importance of functionality for attention and memorization (e.g. Watanabe, 1996).

The results presented in Chapter 4 contradict findings of a previous study that found no transfer from real-life experience with humans to pictures of the same humans (Dittrich et al., 2010). However, this may be mainly due to methodological differences between the studies. Dittrich et al. (2010) found no effect of previous encounters (namely with particular human feeders) on the number of sessions that the birds needed to reliably discriminate between pictures of familiar and unfamiliar humans, but the authors did not test for the transfer of reliable discrimination to pictures of novel familiar humans. It might well be that it took the pigeons some time and effort to extract the class-binding feature (i.e., familiarity) in a context that differed considerably from the one in which they encountered familiar humans in real life, but that, once learned, the discrimination could well be transferred to novel instances. As indicated by the similar length of acquisition phases for birds with and without real-life experience in Chapter 3, acquisition of the discrimination between complex stimuli by means of rote learning and the recognition of the class-binding function might be equally demanding for the birds.

Whereas the investigation of familiarity-based functional classes provided positive results in Chapter 3 and 4, previous studies on the impact of pre-experience with places on the recognition of pictures thereof were inconclusive (Kendrick, 1992; Wilkie et al., 1992; Dawkins et al., 1995). As pigeons navigate and orientate in space, the lack of the 3rd dimension may have well contributed to these inconsistent findings. Spatial orientation is not the only context in which the 3rd dimension is supposed to affect recognition and the lack of the latter in pictures might hamper birds' categorization of a variety of stimuli or at least lead to uncertainties in the interpretation of especially negative results (e.g. Weisman, 2010).

Holograms provide a promising alternative to the use of pictures and Chapter 5 presents first results with this novel kind of stimuli. The experiments summarized in this chapter used artificial stimuli, namely Greebles (Gauthier & Tarr, 1997), to investigate pigeons' and humans' ability to generalize to novel viewpoints of learned real objects and holograms and to assess the equivalence of perceptual information in both stimulus types. Similar as with the inanimate objects in Chapter 3, the use of Greebles ensured a similar amount of stimulus exposure across individuals, as Greebles are artificially created stimuli that are not encountered by pigeons usually. The use of holograms and the Multi-stimulus box (Steurer et al., 2012) offer the opportunity for direct comparisons in visual research with a wide range of different species including investigations on the impact of the 3rd dimension on object recognition and discrimination.

In conclusion, the mechanisms and cognitive limits in the formation of functional classes in pigeons are far from being fully understood but the experiments reported in the present thesis have contributed empirical data that shed light on previously neglected aspects. Although much is known about pigeons' visual perception and discrimination abilities, these birds still provide a fascinating species for further investigation. As Lea (1984) pointed out, because pigeons are phylogenetically distant to humans, the risk of over-interpretations of their abilities due to an anthropomorphic viewpoint is comparably low. Nonetheless, we should not underestimate pigeons' cognitive capacities only because some aspects of "higher" cognitive levels have previously been found only in primates or corvids. Further experiments that apply a methodological approach that takes carefully into account the pigeons' perceptual predispositions and the ecological conditions under which their perceptual and cognitive abilities may have evolved will help to understand better how pigeons selectively attend to, efficiently reduce, and appropriately respond to external information.

FURTHER PROSPECTS

Future experiments that could build on and extend the results presented here may, for example, address the level of categorization in predator recognition with particular focus on relational classes. Based on the findings reported in Chapter 2, different consequences that may result from encounters with different predator types (e.g. terrestrial vs. aerial) may lead to the formation of different sub-classes within the functional class "predator". Hence, same/different relations (e.g. Cook, 2002) between predator cues in different sensory modalities, including the impact of e.g. olfactory information (Krause et al., 2012), could be addressed with different types of predators. Furthermore, although there is convincing evidence that pigeons rely on previous real-life experience in the recognition of humans (Aust & Huber, 2010b), little is known about how pigeons learn about predators. Whether the recognition of threats is innate or learned, which kind of pre-experience the birds need to summarize predatory cues to functional classes and if functional class formation develops with age have, so far, remained unknown. Long-term studies that control for different levels of experience with predators and exposure to simulated threats in captivity might be combined with field studies that investigate naturally occurring events of predation during the ontogeny of individuals. Birds with diverse kinds of experience could be tested for functional class formation within different age classes. Within age classes, different levels of experience might include birds with no prior experience with predators, those that have observed predation on conspecifics (thus further investigating the impact of social learning on predator recognition and avoidance), pigeons that were exposed to predatory cues that indicated different levels of urgency (e.g. different heights in the presentation of visual predator models) and free-living individuals that naturally encountered predators.

To clarify whether pigeons are also able to discriminate at even more specific levels than familiarity, the birds could be tested for “true” individual recognition (Tibbetts & Dale, 2007). For this purpose, individual-specific features should be recognized and matched in different sensory modes and in different contexts, thus indicating categorization that is not based on the common function of perceived cues but on individual-specific characteristics. This may be achieved by testing pigeons for the cross-modal transfer of knowledge about the reliability of food provision by humans. The experimental approach could comprise a first acquisition phase, in which visual facial cues of humans have to be learned in a context of reliable food provision (with human subgroups that consist of reliable and unreliable feeders) and a second acquisition phase in which the birds have to learn about the association of facial cues and individual acoustic features of human voices in a context that is decoupled from food delivery (e.g. by mere human presence). Afterwards, a test phase could follow in which human facial cues are occluded and only acoustic cues are given to the birds. If the pigeons successfully learned about the reliability of food provision by individual humans and matched individual features cross-modally in the acquisition phases, they should be able to discriminate individual humans on the basis of acoustic cues alone in the test phase. The recognition of humans and the inference of reliable food delivery by means of features that were transferred but not associatively learned (namely individual human voices) could be evaluated for example in a task that requires the birds to discriminate between reliable and unreliable humans talking to them (e.g., in a two-choice task).

Because the use of holograms is completely new to animal cognition research, the range of potential future experiments is extensive. Novel approaches may include the investigation of pigeons' discrimination abilities in wavelength ranges that are beyond human vision but match pigeons' spectral sensitivity (Emmerton & Remy, 1983; Campenhausen & Kirschfeld, 1998), including the UV part of the spectrum. Furthermore, holograms may, for example, provide further insight into the impact of motion on the recognition of objects in pigeons. Previous studies on humans have provided evidence that additional information, which is provided by motion, facilitate object recognition relative to static images of different viewing angles (Vallortigara et al., 1988; Vuong & Tarr, 2006). In contrast, reports of this effect in pigeons are inconsistent, providing support for the facilitating effect of motion on object recognition (Emmerton, 1986; Shimizu, 1998) or showing no effect of rotations

(Loidolt et al., 2006; Kramer, 2010). This may be mainly due to the kind of stimulus presentation that is usually used, namely movies, which are rapid sequences of static 2D-images. Rotating holograms, which represent actual physical (i. g. smooth) 3D-rotations may provide a promising solution here.

In conclusion, the present results on functional class formation in pigeons support previous findings on the birds' extraordinary visual discriminative abilities and their capacity to infer equivalence among class members that transcends perceptual similarity. More surprising, even with a profound basis of previous empirical work on how pigeons *see* and classify the world, this species seem to be far from fully understood in how they *interpret* the world. Although pigeons are not expected to possess elaborate cognitive skills comparable to those in e. g. corvids and parrots, the birds tested here demonstrated context-dependent behavioural flexibility and advanced cognitive traits. This might open up the possibility that reported differences among species regarding their cognitive capacities at least partly result from an experimenter-based preselection of investigated species (or experimental set-ups that did not match the target species' perception or ecological background) instead from the genetically determined 'cognitive superiority' of some species.

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CURRICULUM VITAE

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EDUCATION

Since 2009	PhD candidate, Department of Cognitive Biology, University of Vienna, Austria. Supervisor: Prof. Ludwig Huber
2008	Diploma in Biology (equivalent to MA), Department of Biology & Pharmacy, University of Jena, Germany. Major: Ecology, Minor: Botany, Philosophy
2007-2008	Diploma thesis, Supervisor: Prof. Klaus Zuberbühler (School of Psychology, University of St. Andrews, Scotland, UK), Prof. Stefan Halle (Friedrich-Schiller University, Jena, Germany)
2003	Intermediate diploma, Department of Biology & Pharmacy, Friedrich-Schiller University, Jena, Germany

RESEARCH & FIELD EXPERIENCE

Since 05/2012	Research assistant. Institute of Anatomy and Cell Biology, Medical University of Vienna
02-06/2008	Research assistant. School of Psychology, University of St. Andrews, UK: *Vocal flexibility in male Diana monkeys*.
06-09/2007	Student assistant. Project: BIOLOG-DIVA *Plant species richness & composition in grasslands and its impact on herbivorous insects*. Department of Ecology, University of Jena, Germany
01-06/2007	Field work. *Vocal communication in Diana monkeys (*Cercopithecus diana diana*).* Tiwai Island, Sierra Leone

08-11/2004	Field work. Estación Biológica Quebrada Blanco, Peru, *Interspecific associations in tamarins (*Saguinus mystax & S. fuscicollis*).* German Primate Center, Germany
03-08/2005	Student assistant. Project: "*Carbon dynamics of young experimental afforestations in Thuringia*" (doctoral thesis of Axel Don), Max-Planck Insitute of Biogeochemistry. Jena, Germany
05-09/2002	Research assistant. Undergraduate Student. *Predator-prey interactions in insects.* Max-Planck Insitute for Chemical Ecology, Jena, Germany

TEACHING & SUPERVISION

03-08/2013	Lecturer: Practical course in animal cognition - Introduction into the methods of learning experiments with animals. Department of Cognitive Biology, University of Vienna
03-08/2013	Lecturer: Selected topics in Cognitive Biology. Department of Cognitive Biology, University of Vienna
03-08/2013	Lecturer: Human Organ Morphology III (dissection course). Institute of Anatomy and Cell Biology, Medical University of Vienna
Since 05/2012	Teaching assistant. Institute of Anatomy and Cell Biology, Medical University of Vienna; dissection course: *Human Organ Morphology II*
11/2012	design and supervision of a student project on cross-modal individual recognition of heterospecifics in carrion crows (*Corvus corone*) at the Konrad Lorenz-Research Station, Grünau im Almtal
03-10/2011	design and supervision of a student project on contextual modulation of anti-predator behaviour in pigeons in: Practical course in animal cognition - Introduction into the methods of learning experiments with animals. Department of Cognitive Biology, University of Vienna
03-06/2009	Teaching assistant. Journal Club (*Seminar für Master-Studierende, DiplomandInnen u. DissertantInnen im Fachbereich Kognitionsbiologie*) at the Department of Cognitive Biology, University of Vienna
04-07/2003	Tutor: Ökologie einheimischer Säugetiere (Ecology of local mammals), Friedrich-Schiller-Universität, Jena

PRESENTATIONS

12/2012	**Stephan, C.**, Zuberbühler, K. *Coordinated alarm call behaviour in male and female Diana monkeys.* The Association for the Study of Animal Behaviour, Winter meeting. (poster)
06/2012	**Stephan, C**., Bugnyar, T. *Contextual information processing in pigeons.* Animal Cognition workshop at the Ruhr-University Bochum. (oral presentation)
08/2011	**Stephan, C.**, Wilkinson, A., Huber, L. *Individual recognition in a non-social domain – Pigeons recognize individual objects that are ecologically relevant for them.* The Association for the Study of Animal Behaviour, Summer meeting. (poster)
06/2011	**Stephan, C.** *The impact of stimulus quality & visual pre-experience on picture-object recognition in pigeons (Columba livia). CogBio Seminar, University of Vienna.* (oral presentation)
05/2011	**Stephan, C.**, Wilkinson, A., Huber, L. *You choose what you need – the impact of experience on the application of the concept of familiarity.* 2nd Tok Conference of COMPCOG (European Science Foundation Research Networking Programme). (poster)
04/2010	**Stephan, C.**, Zuberbühler, K. *The knowing sex-how male diana monkeys (Cercopithecus diana diana) depend on female referential alarm calls.* The Association for the Study of Animal Behaviour, Easter meeting. (oral presentation)
02/2010	**Stephan, C.**, Zuberbühler, K. *Vocal interactions between sexes in Diana Monkeys* (Cercopithecus diana diana) *& the impact of ontogenetic experiences*. 5th Topical Meeting of the Ethologische Gesellschaft “Communication”. (oral presentation)
06/2009	**Stephan, C.**, Zuberbühler, K. *Complexity of alarm call composition reflects predation*. The Primate Mind: Built to be connected with other minds. Workshop. (poster)
02/2009	**Stephan, C.**, Zuberbühler, K. *Predation increases structural complexity in primate alarm calls.* 4th Topical Meeting of the Ethologische Gesellschaft “Behavior and Evolution”. (oral presentation)
11/2008	**Stephan, C.** *12 pigeons on the holodeck – three kinds of stimulus quality and the pigeon's visual perception*. Privatissimum in Biology of Cognition, University of Vienna. (oral presentation)

INVITED TALKS

03/2013	**Stephan, C.** *Animal Precursors to Human Language: Development, Flexibility and Anatomical Constraints of Signal Production.* Seminar in Anatomy and cell biology. Center of Anatomy and cell

biology, Medical University of Vienna.

02/2013 **Stephan, C.** *The vocal behaviour of Diana monkeys (Cercopithecus diana diana): flexibility and sex differences*. Institut Jean-Nicod - Département d'Études Cognitives, Ecole Normale Supérieure, Paris.

05/2012 **Stephan, C.** *Modelling reality in the field - simulations across sensory modes & the use of robots in the study of animal cognition*. workshop “Using robotic and computer stimuli in animal behaviour and cognition research” at School of Life Sciences, University of Lincoln, UK.

04/2008 **Stephan, C.** *The flexibility in “semantic” signalling in wild Diana monkeys (Cercopithecus diana) in dependency of habitat conditions.* Konrad Lorenz Research Station, Grünau, Austria.

PUBLICATIONS

Stephan, C., Wilkinson, A., Huber, L. (accepted) Pigeons discriminate objects on the basis of abstract familiarity. *Animal Cognition*

Stephan, C., Bugnyar, T. (2013) Pigeons integrate past knowledge across sensory modalities. *Animal Behaviour,* 85: 605-613.

Stephan, C., Wilkinson, A., Huber, L. (2012) Have we met before? – Pigeons recognise familiar human faces. *Avian Biology Research*. 5(2): 75-80.

Steurer, M. M., **Stephan, C**., Aringer, J., Berger, W., & Aust, U. (2012). The Multi-Stimulus box: An innovative learning device for the comparative study on object perception and recognition with various types of stimuli. *Behavior Research Methods* 44 (3): 725-732.

Stephan, C., Pretterklieber, M. L. (2012) Anatomie: zu ausgewählten klinischen Kapiteln. (Anatomy: selected clinical aspects). In: *Bewegung und Leistung, Schmerz* (Motion, efficiency and pain; ed. by G. Stummvoll, M. L. Pretterklieber, F. Kainberger), pp. 360-374. Wien: Facultas.

Stephan, C., Zuberbühler, K. (2008) Predation increases acoustic complexity in primate alarm calls. *Biology Letters* 4 (6): 641-644.

Schwartzberg, E. G., Kunert, G., **Stephan, C.**, David, A., Röse, U. S. R., Gershenzon, J., Boland, W., Weisser, W. W. (2008) Real-time analysis of alarm pheromone emission by the Pea Aphid (*Acyrthosiphon Pisum*) under predation. *Journal of Chemical Ecology* 34: 76–81.

Stephan, C., Steurer, M.M., Aust, U. (under review) Holography as a novel tool for investigating 3D-information processing: Discrimination of holograms and real objects by pigeons and humans. *Journal of Comparative Psychology*

Stephan, C., Zuberbühler, K. (under review) Predation affects call usage but not call structure in female Diana monkeys (*Cercopithecus diana diana*).

PUBLISHED ABSTRACTS

Stephan, C., Zuberbühler, K. (2009) *Predation increases acoustic complexity in primate alarm calls*. Primate Report Special Issue: 37.

GRANTS

12/2012	Research Services & International Relations, University of Vienna, conference grant for the presentation at *The Association for the Study of Animal Behaviour*, winter meeting.
11/2012	ASAB (The Association for the Study of Animal Behaviour) conference grant
06/2012	travel grant from the Ruhr-University Bochum to give an oral presentation at the workshop *Animal Cognition* at the Ruhr-University Bochum
08/2011	Dean's travel grant from the University of Vienna
08/2011	ASAB (The Association for the Study of Animal Behaviour) conference grant
05/2011	COMPCOG (European Science Foundation Research Networking Programme) conference grant for the presentation at the 2nd Tok Conference of COMPCOG
06/2010	Research Services & International Relations, University of Vienna, conference grant for the presentation at *The Association for the Study of Animal Behaviour*, Easter meeting.
06/2009	Department of Neurobiology & Cognition, University of Vienna, conference grant for the presentation at the workshop: "The Primate Mind: Built to be connected with other minds."
05/2009	Research Services & International Relations, University of Vienna, conference grant for the presentation at the *4th Topical Meeting of the Ethologische Gesellschaft*, "Behavior and Evolution".

PROFESSIONAL MEMBERSHIP

International Primatological Society
Association for the Study of Animal Behavior
Gesellschaft für Primatologie e.V.
Ethologische Gesellschaft e.V.
Comparative Cognition Society

LANGUAGES

German, English, French (basic)