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„Rapid discrimination and categorisation of briefly flashed stimuli in the pigeon (*Columba livia*)"

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SUMMARY

Animals' ability to analyse and categorise the visual environment as fast as possible is fundamental, as survival will often depend on the speed with which predators, food, or other relevant objects can be recognised. This study examines the conditions under which rapid visual processing occurs. The outstanding visual discrimination and categorisation abilities of pigeons (*Columba livia*) are well-documented in the literature. However, it is still unclear how quickly these birds may extract the pictorial information necessary to allow for correct classification. In the present study, the pigeons' ability to solve a series of visual classification tasks with severe temporal restrictions was tested. With a modified go/no go- procedure, different types of images — simple geometrical stimuli (Experiment 1) and natural images that either showed or lacked human figures (Experiment 2) — were presented for time spans ranging from 100 msecs to 10000 msecs. Due to this time pressure the pigeons could not extensively explore the stimuli, but were forced to base their category decisions on the very first rapid pass through the visual system.

In most of the tasks the birds succeeded even with very brief presentation times. Nevertheless, discrimination performance correlated positively with presentation time, with the extent of this effect strongly depending on stimulus complexity. Experiment 1 provided evidence that the pigeons were, for the most part, able to correctly classify simple geometric stimuli even when flashed very briefly (100 msecs). Furthermore, discrimination of stimuli differing only in shape was found to be more difficult than that of stimuli differing only in colour. This was reflected by differences between the two tasks regarding acquisition speed and accuracy. These differences were further enhanced by very short stimulus durations. Results were somewhat different in Experiment 2. The subject was well able to classify images with and without humans when shown for 10000 msec. Stepwise reduction of presentation time had, however, considerably stronger detrimental effects than was the case in Experiment 1, and reduction to 250 msecs and less

even led to complete failure. The presentation of novel stimuli provided evidence that also unfamiliar instances of the classes could be categorised, but also this ability was crucially dependent on the time factor: The limit of minimum presentation time at which correct classification was still possible appeared to lie somewhere between two and six seconds.

The results suggest that classification of natural stimuli requires longer presentation times and is thus more prone to failure with very short presentations than is the case with discriminations of simple geometric stimuli.

ZUSAMMENFASSUNG

Zweifellos ist die Fähigkeit, Teile des visuellen Umfelds möglichst schnell zu analysieren, für Tiere von fundamentaler Bedeutung, da ihr Überleben oft von der Geschwindigkeit abhängt, mit der sie Feinde, Beute, oder andere Objekte erkennen. Diese Studie untersuchte daher die Bedingungen, unter denen rasche visuelle Bildverarbeitung auftritt. In der Literatur finden sich zahlreiche Beispiele für die außergewöhnlichen Diskriminations- und Kategorisierungsfähigkeiten von Tauben (*Columba livia*). Allerdings ist nach wie vor ungeklärt, wie schnell diese Vögel Bildinformationen extrahieren können, die für eine korrekte Klassifizierung notwendig sind. Ziel der vorliegenden Studie war es daher, die Fähigkeit von Tauben, verschiedene visuelle Klassifikationsaufgaben zu lösen, unter zeitlicher Beschränkung zu testen. Mittels einer modifizierten „Go/No go"-Prozedur wurden verschiedene Arten von Bildern — einfache geometrische Formen (Experiment 1) sowie Fotografien von natürlichen Objekten (Experiment 2) — für Zeitspannen zwischen 100 und 10000 ms präsentiert. Aufgrund dieser zeitlichen Begrenzung war es den Tauben nicht möglich, die Stimuli im Detail zu erforschen. Stattdessen waren sie gezwungen, ihre Kategorieentscheidungen in erster Linie auf der Basis sehr früher Verarbeitungsmechanismen des visuellen Systems zu treffen.

Die Tauben konnten die meisten Aufgaben auch bei sehr stark beschränkten Präsentationszeiten lösen. Dennoch wirkten sich verlängerte Präsentationszeiten positiv auf die Diskriminationsleistung aus, wobei das Ausmaß dieses Effekts stark von der Komplexität der zu bewertenden Bilder abhing. Experiment 1 zeigte deutlich, dass die Tauben in den meisten Fällen einfache geometrische Formen selbst bei sehr kurzer Präsentation (100 ms) von einander unterscheiden konnten. Des Weiteren konnte gezeigt werden, dass die Vögel Stimuli, die sich nur in der Form unterschieden, schlechter klassifizieren konnten als Stimuli, die unterschiedliche Farben aufwiesen. Dies wurde durch Unterschiede zwischen den beiden Aufgaben hinsichtlich Lerngeschwindigkeit

und absoluter Diskriminationsleistung deutlich, die durch besonders kurze Präsentationszeiten noch weiter verstärkt wurden. Experiment 2 zeigte ein etwas anderes Ergebnis. Zwar konnte das Versuchstier Bilder mit und ohne Menschen bei einer Präsentationszeit von 10000 ms korrekt klassifizieren, doch eine schrittweise Verkürzung der Präsentationszeit beeinträchtigte die Leistung in einem viel stärkeren Ausmaß als dies in Experiment 1 der Fall war. Präsentationszeiten von 250 ms und weniger führten sogar zu einem kompletten Versagen. Die Präsentation neuer Bilder zeigte, dass auch unbekannte Klassenvertreter richtig eingeordnet werden konnten, aber auch diese Fähigkeit war stark vom Zeitfaktor abhängig. Die Grenze, ab der korrekte Klassifizierung möglich war, lag vermutlich irgendwo im Bereich zwischen zwei und sechs Sekunden.

Zusammenfassend zeigen die Ergebnisse, dass Tauben mehr Verarbeitungszeit für die Klassifizierung natürlicher Stimuli benötigen, als für das richtige Zuordnen einfacher geometrischer Formen.

1. INTRODUCTION

"Our spontaneous action is always the best. You cannot, with your best deliberation and heed, come so close to any question as your spontaneous glance shall bring you."

Ralph Waldo Emerson (American Poet, Lecturer and Essayist, 1803-1882)

Analysing our visual world seems to be effortless and instantaneous. Detection, discrimination and categorisation are mechanisms that are used with relative ease and impressive speed. Such abilities are obviously crucial considered from an ecological point of view. Taken out, of course, of its original context, Emerson's quote cited above touches the heart of the matter: it is sometimes vitally important for us to capture information within a single glance. However, other visually-dominant animals face the same visual challenges and have to deal with similar problems when moving about the world. When we imagine what animals may perceive and process we often extrapolate from our own sensory experience of the world. But this might not hold true for other species. Therefore, it is an appealing issue to determine whether a highly visual animal like the pigeon is able to apply comparable mechanisms of rapid detection, discrimination and categorisation as humans.

1.1. Theories of stimulus classification

In this section I want to give an overview of some specific aspects of visual cognition. There are several ways — differing in cognitive demand — in which animals actively evaluate the wealth of information available in visual stimuli, encode these external featural properties into an internal representation and subsequently group them into different classes according to their discriminable properties. These mechanisms can range from mere *perceptual* classification, achieved by discrimination of elementary visual features of the stimuli, to *conceptual* categorisation, which involves symbolic or abstract representations governed by relations between and among concepts (e.g., Herrnstein, 1990; for a review, see Huber, 2001). Generally, the ability to treat similar things as somehow equivalent seems to have an enormous ecological advantage and is therefore elaborated in more detail below. Of course, these grouping mechanisms could also be assigned to discrimination and categorisation capabilities in other modalities than the visual domain (e.g., discrimination and categorisation of auditory and olfactory cues). However, I will focus only on visual stimulus classification in the following.

1.1.1. Visual discrimination

The most elementary level of stimulus classification and lowest in cognitive demand is the level of discrimination (proposed by Herrnstein, 1990). Much research on the visual capacities of birds or animals in general has focused on the ways in which simple visual stimuli are discriminated and divided into artificial classes. One big advantage of using carefully constructed sets of artificial stimuli is that these simple stimuli vary on clearly defined dimensions like colour, texture, or shape and are therefore easy to control by the experimenter. Such studies have involved a variety of different stimulus sets, like letters (e.g., Blough, 1982, 1985; Cavoto & Cook, 2001; Fremouw et al., 2002), simple geometric forms (e.g., Blough, 1972; Cook et al., 1992; Kirsch et al., 2008, Lazareva et al., 2005; Reynolds, 1961), and simple line drawings (e.g.,

Kirkpatrick-Steger & Wasserman, 1996; Peissig et al., 2005, 2006). Studies like these allow for investigations with easily describable experimental materials. Therefore, stimulus structure can be investigated in the context of different questions under controlled conditions. Introducing simplified geometrical figures in a perceptual discrimination task helps to narrow down the number of cues the birds may use to guide their decisions. Of course, pigeons' visual worlds do not consist of these kinds of simplified elementary stimuli. Therefore, studies examining simple forms like spots, lines and shapes, tell us only about one part of stimulus classification. Nevertheless, the discrimination of elementary stimuli is an important prerequisite for higher level mechanisms of stimulus classifications, namely categorisation of natural classes.

1.1.2. Visual categorisation

The biological relevance of categorisation

The natural environment is a huge source of information. Thus, to guide and condensate this sensory overload, an evolutionary adaptation is needed. Drastic reduction of information is a basic principle of cognitive economy and therefore assumed to be widely dispersed among species. Categorisation constitutes an appropriate instrument. In its broadest sense, it can be viewed as the ability to treat similar, but not identical things as equivalent, by sorting them into categories and by reacting to them in the same manner (e.g., Herrnstein, 1984; Huber, 2001; Rosch, 1978). Within a category, class members can thus be defined rapidly without any necessity for the subject to be conditioned to one instance after another. This allows generalisation to members of the class that have never been seen before by applying to them category-relevant knowledge. Between categories, an organism is able to distinguish the important features characterising each class. Categorisation therefore allows rapid information processing, fast behavioural responses and space-saving dynamic storage in memory. Because categorisation is so fundamental and a basic principle of dealing with all kinds of biologically relevant factors like food, conspecifics or enemies, it is assumed that it is present throughout the phyletic scale.

Empirical evidence throughout the animal kingdom

Although the general advantage of categorisation is obvious, research concerning categorisation has for a long time been restricted to human cognition. However, since Herrnstein and Loveland (1964) showed that pigeons were able to show category discrimination, a lively and broad area of research on this topic in animals has developed. Many experiments with species other than pigeons have yielded evidence of the amazing categorisation abilities of a variety of animal species. These include other bird species, like blue jays (e.g., Real et al., 1984), chickens (e.g., Ham & Osorio, 2007; Ryan & Lea, 1999; Jones et al., 2001) and Bengalese finches (Watanabe et Jian, 1993). Regarding mammals, research has mainly been focused on primates, like baboons (e.g., Bovet & Vauclair, 1998), rhesus monkeys (e.g., D'Amato & Van Sant, 1988; Fabre-Thorpe et al., 1998; Santos et al., 2001; Sigala et al., 2002; Vogels, 1999), squirrel monkeys (Roberts & Mazmanian, 1988) and chimpanzees (e.g., Parr et al., 2008; Tanaka, 2001), but also other mammal species have been investigated, like horses (Hanggi, 1999), cattle (Coloun et al., 2007, 2009), sheep (Ferreira et al., 2004; Kendrick et al., 1995), sea-lions (e.g., Reichmuth Kastak & Schusterman, 2002) and recently dogs (Range et al., 2007). Even invertebrate species, like the honey bee (Benard et al, 2006; Zhang et al., 2006), have been in the focus of interest.

Empirical evidence in the pigeon

The domestic pigeon (*Columba livia*) is, as a highly visual and mobile animal, an ideal species for testing visual categorisation abilities. Not surprisingly, a vast body of research on visual categorisation concerns pigeons. Dozens of studies have been conducted since the 1970s and is worth mentioning some of the categories that have been investigated. Though, the examples given here do not attempt to be exhaustive. Research on the ability of animals to categorise was really opened by the pioneer study of Herrnstein & Loveland (1964). Their work revealed the surprising capacities of pigeons to sort natural photographs on the basis of whether or not an image contained a human being. The pigeons were trained to peck a key for reinforcement in the presence of pictures that contained a person and to refrain from pecking in the presence of

pictures that did not (for a review see, Huber & Aust, 2006; Watanabe et al., 1993). It could be shown that the birds learned easily and generalised widely. Many experiments following this initial one have demonstrated that Herrnstein and Loveland's results were quite general and could be replicated with completely different classes of stimuli, ranging from artificial classes such as line drawings (Huber & Lenz, 1993) and cartoon characters (Cerella, 1980), to natural classes using complex stimuli. In the following, I will only refer to studies that employed complex natural stimuli. Among the categories that have been learned are human artefacts vs. natural objects (Lubow, 1974), trees (Herrnstein et al., 1976), chairs, cars, humans and flowers (Bhatt et al., 1988; Lazareva et al., 2006), birds and other animals (Roberts & Mazmanian, 1988), human faces (Huber et al., 2000; Loidolt et al., 2003; Jitsumori & Yoshihara, 1997; Troje et al., 1999) and conspecifics (Nakamura et al., 2003; Shimizu, 1998, Wilkinson et al, in press).

Of course, there were also a lot of studies that directly continued the groundbreaking research of Herrnstein and Loveland on "person/non person" categorical discrimination (Aust & Huber, 2001, 2002, 2003, 2006, 2009; Greene, 1983; Malott & Siddall, 1972; Siegel & Honig, 1970). As a consequence of their findings Herrnstein & Loveland concluded that pigeons' categorisation abilities are based on a generalised "concept" rather than on simple features or on rote learning, and the available evidence indeed seemed to suggest abilities that go far beyond simple discrimination of stimulus dimensions, such as wavelength, intensity and frequency (see Honig & Urcuioli, 1981). More recent evidence suggests, however, that this interpretation has been a bit premature because we do not know whether pigeons indeed have concepts and use them to solve category problems (for a review, see Huber & Aust, 2006). But what could then be the mechanism underlying a "person/non person" concept discrimination?

In fact, there are various possible ways and strategies that might be working (for a review, see Huber, 1999, 2001, 2009). However, concerning the account of "person/non person" categorisation, a modified version of a *feature theory* might be appropriate (for a comprehensive definition of this theory, see

Huber & Aust, 2006). This modified approach assumes that categorisation may be based on various types of features and different ways of processing them. As a consequence, stimulus perception, feature selection and processing mode strongly depend on the specifics of a particular task. Therefore, different and sometimes partially divergent types of features coexist in a pigeon's internal representation and can be flexibly used, depending on the experimental situation. The available evidence suggests that pigeons store different types of information in parallel during learning. For example, Aust and Huber (2001, 2003) found that both types of information - *item-specific* as well as *category-specific* – were stored in parallel during learning. Item-specific discrimination is defined as a strategy that relies on tiny idiosyncratic stimulus aspects or pixel properties, a mosaic-like perception of a visual scene, which may even allow identification of strongly scrambled versions of familiar stimuli. The second strategy — category-specific discrimination — involves attending to class-distinguishing stimulus features such as specific parts or configural aspects that are common to the embedded targets. Likewise, both global and local levels of processing can be used, but the specifics of a task determine what type of processing will prevail (Aust & Huber, 2001). Global features, as characteristics of the whole stimulus (such as size, orientation and brightness) are computed automatically and in parallel at every location of the visual field (cf., Treisman & Gelade, 1980). Local features, in contrast, are restricted semiautonomous portions of a stimulus (e.g., such as the head, nose, eye of a human figure) which are processed serially. That is, one item and one location at a time will be coded. Aust and Huber (2001) could show that pigeons still discriminated scrambled versions of stimuli, based on the computation of small local identification elements (but see Troje et al., 1999; Huber et al., 2000. There, subjects' classification ability was rather based on using colour, overall intensity, and shading information. Consequently, neither blurring nor presenting block portraits led to any significant disruption of classification ability). Obviously, pigeons are quite flexible in their use of strategies when acquiring a natural categorisation task. The acquisition of knowledge about a stimulus to identify is dependent on the specifics of a task. Accordingly, the challenge of a particular task and the wealth of the stimulus determine the strategy that will be used.

1.1.4. Rapid discrimination and categorisation

"Reasons to be fast"

The ability to analyse the visual environment rapidly is without doubt an important and critical component of biological visual systems. The survival of an animal often depends on the speed with which predators or food can be detected and recognised. Therefore, various biologically relevant scenes that suddenly appear within the current field of view have to be discriminated and categorised quickly. (1) As pigeons in nature typically forage in groups (Levebvre, 1985), individuals are often forced to search for food under highly competitive conditions. Pigeons are granivorous, which requires intensive and efficient foraging, because potential competitors may shorten the available time (Plowright & Landry, 2000; Sol et al., 1998). A pigeon thus ought to be quick to identify the spatial location and properties of the target seed to pick up food before the competitor does so. (2) A second biological constraint that enhances rapid discrimination and categorisation is to notice sudden attacks by predators. Antipredator behaviour (e.g., escape behaviour) is expected to be under strong selection. Therefore, rapidly looming and suddenly appearing objects like approaching aerial predators have to be detected and identified as fast as possible. Indeed, time for predator detection and identification is limited by the need for rapid and accurate response (Wang & Frost, 1992). (3) Finally, with the added dimension of rapid flight, birds may be especially adept in processing flashed natural scenes when moving through the air at high speed.

Empirical evidence throughout the animal kingdom

Currently, a growing literature on (ultra-)rapid categorisation has demonstrated that human and nonhuman primates are very efficient in detecting animals, fruits or other target categories in natural scenes. They proved capable of rapid and accurate categorisation of natural images presented down to 20 msecs in studies with human subjects (e.g., Fabre-Thorpe et al., 2001; Fei-Fei et al., 2007; Li et al., 2002; Rousselet et al., 2003, 2005; Thorpe et al., 1996, VanRullen & Thorpe, 2001), and down to 30 msecs in studies using rhesus monkeys (e.g., Delorme et al., 2000; Fabre-Thorpe et al., 1998; Macé et

al., in press). The general procedure applied in these studies is based on a go/no-go task that involves the very brief presentation of single images. Participants/subjects have to respond manually by releasing a button if they detect a target (Thorpe et al., 1996). Human participants usually scored over 90% correct, with minimum reaction times around 250 msecs. Monkeys achieved scores of approximately 90% correct with minimum reaction times of 180 msecs. More recently, a choice saccade paradigm has been introduced. In a choice saccade task, two photographs of natural scenes are flashed for a short time period left and right of fixation while human participants or monkeys are asked to make a saccade to the side of the target object (Kirchner & Thorpe, 2006; Girard et al., 2008). Both, monkeys and humans, performed at high levels of accuracy, with minimum reaction times of 100 msecs, and they were also able to generalise to new stimuli.

A number of surprising results have emerged from these studies. First, rapid categorisation does not require foveal vision, and images can be presented randomly at different eccentricities without decrements in accuracy (Fize et al., 2005; Thorpe et al., 2001), and even in the near absence of spatial attention (Fei-Fei et al., 2005; Li et al., 2002). Second, the presence of colour information is not necessary for this form of rapid visual categorisation (Delorme et al., 2000). Third, there is no impairment in processing upright and inverted natural scenes (Rousselet et al., 2003). Fourth, categorisation is quite robust to reducing contrast levels (Macé et al., 2005, in press). Finally, rapid reaction times cannot be shortened by familiarity with the stimulus images — not even with intensive training (Fabre-Thorpe et al., 2001). These results are quite astonishing. Categorisation performance is still surprisingly good and appears remarkably similar in human and non-human primates, even when severe time constraints force the subjects to make rapid decisions on the basis of the first rapid pass through the visual system.

Empirical evidence in the pigeon

Compared to the primate literature, evidence of pigeons' rapid processing abilities is rather sparse. There are some studies (e.g., Brown, 1991, Brown & Morrison, 1990; Cook et al., 1992; Guttenberger & Wasserman, 1985; Mac Donald, 1993; Maki & Leith, 1973), that varied lengths of stimulus presentation to investigate discriminative responding in a (delayed) matching-to-sample (MTS) paradigm (see Blough, 1959). There, the subject animal performs in a three-key operant chamber and has to choose the comparison stimulus that is consistent with the sample stimulus presented previously. What these experiments had in common was the use of simple geometric shapes that had to be matched. All studies cited above could show that performance varied directly with stimulus presentation time, irrespective of which kind of task had to be solved. Concerning studies applying other types of procedures, research is almost entirely missing so far, with only a few exceptions. Cook and colleagues (1997) tested pigeons on texture displays that rapidly and dynamically changed their relevant properties within the course of a single presentation. These dynamic trials used a modification of the rapid serial visual presentation (RSVP) procedure frequently used in perceptual research with humans (e.g., Intraub, 1980). On these dynamic RSVP test trials, the elements defining the display changed colour and/or shape at regular intervals within a single trial. The authors found out that pigeons can perceptually group and segregate texture differences quite rapidly. Processing of global and local information by pigeons was tested with hierarchical "letter-stimuli" shown under temporal constraints with a four-alternative choice procedure (Cavoto & Cook, 2001). After the presentation of one of four stimulus conditions four choice stimuli appeared each in a separate corner of the screen. The pigeons' task was to choose the choice stimulus associated with the relevant letter presented on that trial. Diekamp et al. (2002) investigated delay activity of single neurons to test for working memory in a go/no-go procedure. There, the pigeons had to perform a simple discrimination task with stimulus presentation times of 500 msecs, and succeeded. Stimuli that were more challenging regarding complexity were used in a study where same and different arrays had to be discriminated (Wasserman

et al., 2002). There, the pigeons were tested with reduced exposure to the pictorial arrays in a symbolic matching-to-sample task. In each trial a "same" or "different" icon array was turned on. After a fixed presentation time two report areas appeared. Pecks to the red report area on same trials and to the green report area on different trials were correct and were reinforced. Two seconds of processing time were found to support reliable discrimination. Natural stimuli, however, have only been investigated in three studies involving shortened presentation times. Cook and colleagues (Cook & Blaisell, 2006; Cook et al., 2003) used a go/no-go procedure to study the "same/different" concept. There, two different or two identical colour photographs (shown for 500 msecs/1000 msecs) where shown in succession in a sequence of either identical (AAA. . . = same trials) or different (e.g. ABAB. . . = different trials) stimuli. Finally, the effects of stimulus duration and choice delay on visual categorisation have been investigated by using presentation times of one, five and ten seconds in two/four-alternative choice procedures (Lazareva & Wasserman, 2009). Results again indicated a significant effect of stimulus duration on performance.

1.2. The visual capacities of pigeons

1.2.1. "The avian eye view"

Birds are visually-dominant organisms. Because they forage, mate, have to avoid predators and, of course, fly, they need very accurate descriptions of the three-dimensional visual world around them. They have to visually identify objects as quickly and accurately as possible. Nature has therefore equipped them with a set of visual capabilities that are in some cases even superior to those of humans (e.g., Hodos, 1993). Concerning pigeons, physiological measurements indicate that the critical flicker fusion frequency is approximately 140 Hz (Hendricks, 1966), whereas it is only 60 Hz for humans. They have two specialised areas, or foveae (*area dorsalis* and *fovea centralis*), which may have different functions (cf. Hodos, 1993; see Cook, 2001). Studies comparing lateral and frontal viewing have shown that while frontal acuity

decreases with distance, lateral acuity increases with distance (Bloch & Martinoya, 1982; Rounsley & McFadden, 2005). Pigeons thus seem to be well adapted to both visually guided frontal tasks at near distances (feeding, landing) and visually guided lateral tasks at far distances (warning). Considering these extraordinary visual capacities, it is rather unlikely that their perception should fail with rapidly presented stimuli. Some capacities might even make pigeons more sensitive to rapid events, like their high flicker fusion threshold.

1.2.2. Methods of rapid stimulus presentation

Researchers that investigate the influence of temporal factors on behaviour usually use controlled stimulus presentation times for their research questions. They use stimuli that are shown *tachistoscopically*. This means that the images are flashed with great speed and brief views of the stimuli can be provided. Therefore, they have developed during the last decades a wide variety of procedures and apparatuses to precisely control time-dependent processes in laboratory environments. Most of their research has been focused on human neuropsychological questions. The earliest studies are dating back to the beginning of the last century (Dallenbach, 1923). Among the earliest experimental devices were "gravity drop" tachistoscopes, followed by mechanical shutters, electronic shutters, projectors, and, finally, computer-controlled monitors (for a review, see McKeever, 1986).

Although there is great variety how temporal factors are tested in the literature, there are generally four main factors that affect the ability to determine the actual timing of stimuli. First, *control devices* have to determine stimulus duration as accurately as possible. Second, *presentation devices* are needed that generate the stimulus with all of its properties, to, third, eventually project it onto an appropriate *display area*. Fourth, it is important to minimise delays that occur through *communication* (e.g., data transfer and file sharing) between the aforementioned devices.

These requirements have been dealt with in different ways. A lot of studies, especially in the early years of research, presented images by means of a

"tachistoscope" (e.g., Marcel, 1983, Intraub, 1980; Navon, 1977; Sperling, 1960). The tachistoscope, which was invented by Volkmann in 1859 (see, Tsai, 2001), is an instrument for brief exposures of visual stimuli in experimental psychology. For the most part the tachistoscope is connected to a projector that projects the stimuli onto a screen or onto keys. The use of microcomputers and computers for stimulus control was the next step in improving experimental designs. The stimuli were mainly presented with projectors onto a screen or keys, the onset and the offset of a stimulus was mainly accomplished by shutters (e.g., Brown, 1991; Cook et al., 1992; Langley & Riley, 1993; Potter, 1976; Maki et al., 1976). Today, computers have almost entirely replaced the former presentation methods (e.g., Fabre-Thorpe et al., 2001; Fei-Fei et al., 2007; Li et al., 2002; Rousselet et al., 2003, 2005; Thorpe et al., 1996, VanRullen & Thorpe, 2001). The benefits of using computers to control tachistoscopic displays are efficient stimulus preparation, the possibility to display a large number of complex visual stimuli without effort, ease of collecting data for analysis, and flexibility in sequencing stimulus presentations. To control for accurate presentation times, many computers are equipped with control software (e.g., Presentation® software, e.g, Macé et al., 2009). However, some studies have based their timing calibrations on standard PC hardware alone. As display devices, computer monitors (CRTs or LCDs) have been adjusted. For years, the CRT (Cathode Ray Tube) monitor had been the dominant display technology. Recently, however, new display technologies have grown such as LCD (Liquid Crystal Display) monitors. Thereby, it has to be noted that perceived image quality can be strongly influenced by display type (for a review, see Krantz, 2000). LCDs differ from CRTs in several respects, with both bearing advantages and disadvantages. For instance, CRT monitors present continuously alternating lines of brightness information on the screen, which might be perceived as "flickering" by birds, considering their high threshold of flicker fusion frequencies (Emmerton, 1993; D'Eath, 1998). The refresh rates of LCDs are normally twice as high as those of CRTs (Gibson et al, 2004), thereby reducing problems associated with "flickering". Furthermore, LCDs are superior over CRTs regarding sharpness, resolution, contrast, luminance, and absence of geometric distortions (Elze, 2007). Additionally, subjects' error frequency was found to be lower for LCDs in

a visual search task (Menozzi et al., 2000). In contrast, CRT monitors outperform LCDs when moving stimuli are presented, for example, with respect to motion blur (Tourancheau et al., 2008). In addition, the persistence of visual stimuli on some LCD displays with longer response rates (this refers to how quickly a pixel can change colours, measured in msecs), may cause troubles, especially when stimulus durations have to be controlled precisely. However, Rovina (2006) found no differences in pigeons' performance depending on stimulus presentation on the two types of monitors (LCD *vs.* CRT).

To conclude, all these different experimental set-ups lead to some variation in how the stimuli are generated, which may be a source of error in timing a stimulus. Additionally, it effectively could happen that due to severe time constraints stimuli are not presented intact, especially when CRT-monitors are used. It might therefore be better to bypass the problem of inexactness by not reducing stimulus presentation time too strongly, especially if the procedural devices can't guarantee precise timing. Furthermore, comparisons of experiments employing different methods and technical equipment have to be viewed with caution.

1.3. The aim of the study

The present study was carried out in order to answer the following questions: (1) Would a pigeon's performance be affected if discriminative stimuli were varied in duration? (2) Where are the temporal limits of pigeons' rapid categorisation abilities? (3) Do severe temporal constraints influence categorisation of different types of target images, varying in complexity, to different extents? And, if so, what may be the reasons for these differences? (4) How efficient is the Rapid Categorisation paradigm used in the present study in investigating pigeons' responding in a variety of tasks but with identical procedural parameters? To investigate these issues I conducted two experiments (Experiment 1, "geometric figures" and Experiment 2, "natural stimuli").

2. GENERAL METHODS

2.1. Subjects

The experiments were conducted with pigeons (*Columba livia*) of a local Austrian race ("Strasser"), and homing pigeons (Figure 1). The two breeds considerably differ from each other in terms of their body size and weight. Homing pigeons are smaller sized and swifter than their heavy and slow counterparts. Concerning their behaviour the "Strasser" pigeons tend to be more balanced and willing to peck, as described in previous studies (e.g., Huber & Lenz, 1993, 1996; Troje et al., 1999). Although it should be necessarily kept at the back of one's mind that hereditary differences can have an effect on visual anatomy or functions (Jahnke, 1984), to our knowledge and experience, however, there are no differences regarding their cognitive and visual abilities.
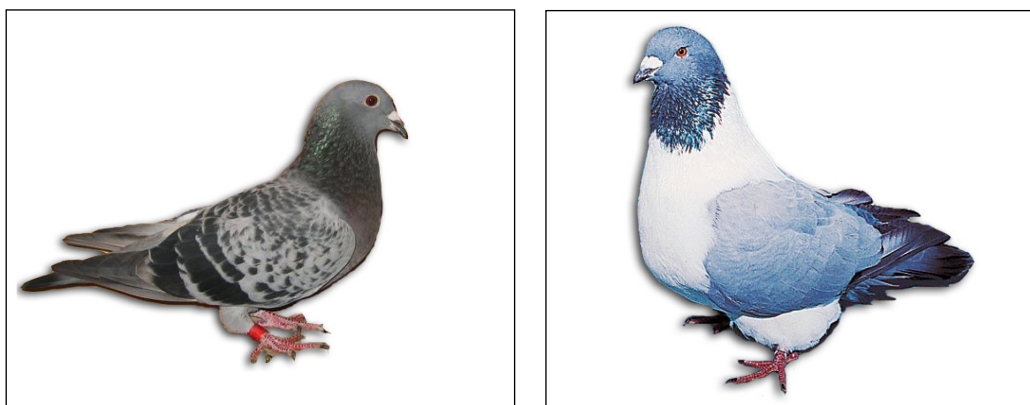
Figure 1   Illustrations of the two pigeon races used, without considering size proportions. Left: homing pigeon, right: Strasser.
(Edited pictures of source: http://www.siegfried-meyer.de and http://www.fermedebeaumont.com)

The birds I used for the experiments were housed together with several conspecifics in a large outdoor aviary, which was divided into five compartments, each measuring 3.0 x 1.20 metres. Only at the time of testing the subjects were separated from their group members. The pigeons had free access to water and grid in their home cages, whereas food (standard grain mixture

consisting of 35.0 % french maize, 20.0 % wheat, 15.0 % yellow peas, 10.0 % green peas, 10.0 % milo, 5.0 % maple peas, 2.5 % dari and 2, 5 % cardy / safflower seed) was offered only during experimental sessions and as supplement immediately after finishing the session. On non-testing days the pigeons were supplied with extra rations of food. The birds were maintained at free-feeding weights slightly reduced to encourage through hunger their motivation to work. All the birds were familiar with the experimental chamber and the procedure, due to the fact that they had already participated in a series of previous discrimination and categorisation tests. They were, however, naive regarding people-present/people-absent discrimination tasks.

In Pretraining and most of Experiment 1 two "Strasser" (T6, T44a) and six homing pigeons (B2, B10, B22a, B23, B33, and B34) were employed. As I decided to use only the most promising and motivated pigeons further on, only the two "Strasser" (T44a and T6) and three of the homing pigeons (B22a, B10, and B34) proceeded to the last test of Experiment 1, and only two birds (B22a and T44a) took part in Experiment 2.

2.2. Apparatus

The experiment used two specially constructed operant chambers ("Skinner Boxes"), which the pigeons entered via a particular pass way system, developed in our lab (Huber, 1994) and successfully used in a series of studies (e.g., Aust & Huber, 2001, 2002, 2003). Thereby, they could get through a connecting passage from their outdoor aviary compartment directly into the Skinner boxes in the lab. All the experiments were conducted in these two identical boxes (50 x 30 x 40 cm in size). A simplified drawing of the operant chambers used is shown in Figure 2.
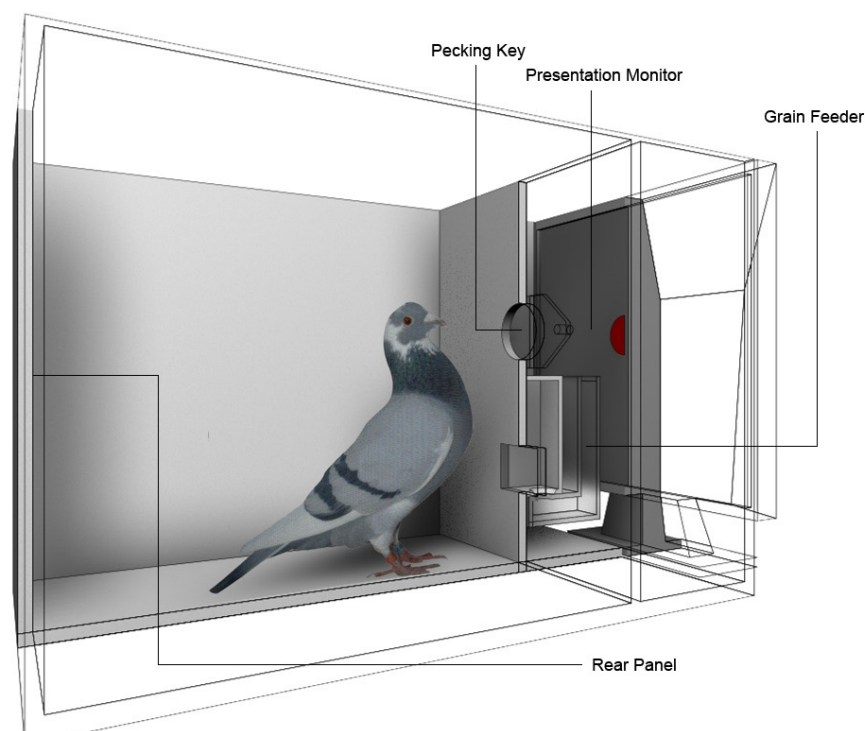
Figure 2   Schematic drawing of the operant box used during the study. For reasons of clarity the chamber is cut in halves. The subject facing the intelligence panel evaluates the stimulus presented on the monitor, peeping through the transparent pecking key in the front wall. Find proper explanations of the chamber's structural elements in the main text.

The inner front wall of each wooden chamber was designed as "intelligence panel", consisting of two elements:

(1) A *transparent Perspex pecking key* (5 cm Ø; ENV-125M, MED Associates, Georgia, Vermont) was affixed to the middle of the front panel of the box, 28 cm above the floor. Any dislocation of the pecking key caused interruption of an electric contact and could be registered by a connected PC. (2) Through an opening at the bottom of the panel the pigeons had access to a 28-V DC solenoid activated food hopper of a *grain feeder* (ENV-205M).

The chamber was dimly lit by a 2W-house light (ENV-215, Med Associates, Georgia, Vermont) in the rear part of the box throughout the experimental sessions. Only during a 4 sec intertrial interval that preceded stimulus presentation the chamber was completely dark. A hopper light offered additional illumination during food delivery. Two PCs were used for each chamber. They were equipped with a digital input/output board with Keithley-

Interfaces and a special software package that selected the patterns according to a pre-specified sequence (PigeonLab©; Steurer, 2002). Furthermore, it controlled all events during the experimental sessions, such as stimulus duration, food delivery and recording of the pigeon's responses, which implied counting pecks emitted solely during stimulus display as well as during the whole ten seconds of recording. Each computer was connected to a presentation LCD monitor (Videoseven L15C; 15-inch screen diagonal; resolution 1024 x 768; pixel pitch .297 mm x .297 mm; response time 35 msecs) and to a corresponding control monitor that allowed observation of the operational sequence. All images were presented at a size of 45 x 45 mm (resolution 28.35 pixels/cm) on the LCD monitor at a distance of five centimetres behind the transparent pecking key.

2.3. Stimuli

The stimuli I used in my study can be divided into two types according to their complexity. In Pretraining and Experiment 1, simple monochromatic *geometric figures* served as stimuli, whereas in Experiment 2, complex *natural stimuli* were shown to the subjects. As regards the geometric figures the stimuli were plain forms such as letters or circles designed with the Microsoft program Paint©. The complex natural stimuli were full-colour photographs, selected from the pool of images used in the "person/non person concept" studies by Aust and Huber (2001, 2002, and 2003). Half of these photographs showed one or more persons, whereas the other half did not. The various types of stimuli will be described in detail in the method sections of the respective experiments. The stimuli, all at a size of 45 x 45 mm (128 x 128 pixels), were presented at a monitor resolution of 1024 x 768 pixels on the black computer screen. Table 1 (page 26) gives a brief overview of the stimuli used in the different parts of this study.
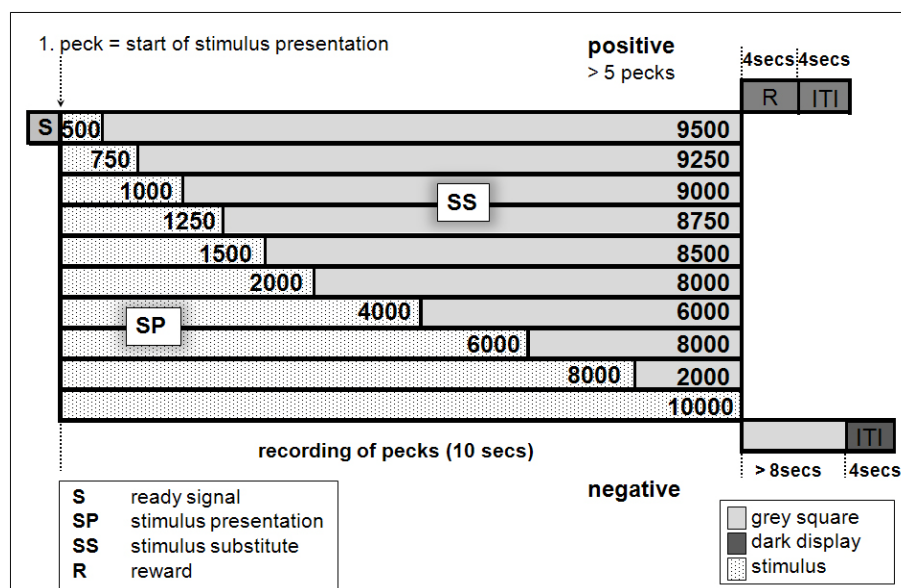
2.4. Procedure

Because the subjects had participated previously in a couple of similar experiments, they were already able to enter the operant chamber voluntarily, and to work in a so called standard go/no-go procedure (Vaughan and Greene, 1984). This method, well-established in our lab, was successfully used in a considerable number of studies (e.g., Aust & Huber, 2001, 2002, 2003; Huber & Lenz, 1993, 1996; Huber et al., 2000; Loidolt et al., 2006) to test for discrimination and categorisation capacities of pigeons. It takes advantage of *positive* and *negative reinforcement* methodology (*operant conditioning*; Skinner, 1938) insofar as a reinforcer (food) strengthens the desired response (pecking in the presence of positive stimuli) whereas punishment (absence of food delivery and a delay interval) reduces responding (i.e., the pigeons withhold pecking when a negative stimulus is shown). The use of a successive go/no-go procedure allowed for graded responses that may be more sensitive to small changes in associative strength than a discrete choice measure. Each subject participating in my study had to execute a work schedule of one session a day, five days a week. A session consisted of 40 trials, invariably comprising twenty "go" trials (presentation of a positive stimulus, S+) and twenty "no-go" trials (presentation of a negative one, S-). In training sessions, the trials were merged randomly and automatically by the computer program (PigeonLab; Steurer, 2002), but in compliance with the rule that no more than three stimuli of the same contingency were shown in immediate succession. Regarding test sessions, twenty novel pictures (ten positive and ten negative ones), were interspersed at pre-specified positions into ordinary training sessions. The first stimulus in every session was always a positive one. Because I used briefly flashed stimuli, I had to modify the standard go/no-go procedure and change it into a "rapid categorisation procedure"(RC procedure).

When the subject entered the box, the session was initiated by starting the computer program. Each trial began with the presentation of a starting signal, a grey square (45 x 45 mm in size), which the pigeons had to peck once to

produce stimulus presentation. Following this, the stimulus was presented and remained for a prespecified time (presentation time) that could last from 100ms to 10000ms, depending on the settings of the individual tasks. Pecks were counted and registered in each trial for data analysis during the first 10 sec after initialising stimulus presentation (counting interval). As presentation time was, for the most part, shorter than 10 sec, I had to introduce a stimulus substitute that was immediately displayed after stimulus presentation. It served as a surrogate for the original stimulus until the counting interval was over and thereby provided the pigeons with a target towards which they could direct pecks after the stimulus had disappeared from the screen. I decided to choose the same grey square that was used as starting signal to prevent the subjects from considering it an additional further stimulus they had to classify. If the pigeons did not peck at least five times within the counting interval on *positive trials*, presentation of the substitute was prolonged until a total of five pecks had been delivered. In this case, the fifths peck darkened the display area and resulted in four seconds of food delivery. If the pigeons pecked at least five times already during the counting interval, food was administered immediately after the first ten seconds of presentation. The 5-pecks-requirement was established to enhance pecking during the counting interval. On *negative trials*, presentation of the stimulus substitute interval was extended until the subject stopped responding for at least 8 sec. In negative trials no reward was delivered. Each trial was followed by a four seconds intertrial interval (ITI), a dark phase that signalled the forthcoming of the next trial. Schematic assemblies of an experimental trial are shown in Figure 3.

A

B
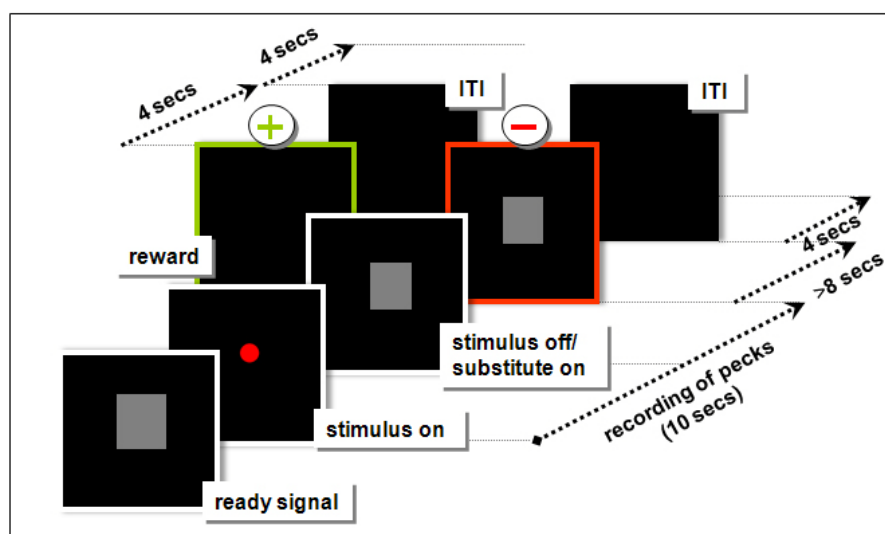
Figure 3   Schematic diagrams of one trial of the experimental RC procedure. Sequence of display changes is depicted, starting with the starting signal and ending with the intertrial interval (ITI). The positive contingency is shown in the best case scenario, meaning that the subject pecked at least five times during the ten seconds of peck recording. (A) The various presentation time spans (in msecs) of stimuli and stimulus substitutes are depicted (Training condition of Experiment1). (B) For better understanding, positive and negative contingencies are marked with green and red frames as well as plus and minus.

Stimulus contingencies and the order in which the One-Component-Different tasks of Experiment 1 were carried out were counterbalanced across subjects. Table 1 gives an overview of the individual phases of both experiments as well as the training history and the positive reinforcement contingencies of each bird. Furthermore, it depicts examples of the stimuli used in the whole study. Namely, it shows examples of stimuli that were positive for each subject in Experiment 1 (Pretraining: either the blue square or the red circle; Two-Component Different training: either the purple "O" or the orange "A"; One-Component Different training: either the aqua or the maroon "question mark", and either the silver arrow or the silver heart) and in Experiment 2 (either person present or person absent). Table 1, however, just provides an overview of each subject's experimental history. Find proper explanations in the methods sections of the respective experimental parts.

Table 1.
Order of experimental phases for each bird, including examples of positive stimuli.

| Subject | Testing Sequence | | | | | | | | | |
	Experiment 1							Experiment 2		
B2	P ▢	TCD O	OCDc ?	OCDs ⬌						
B10	P ▢	TCD O	OCDs ?	OCDs ♥	T O					
B22a	P ⬤	TCD O	OCDs ⬌	OCDc ?	T O	CT1 🖼	CT2 🖼	GT 🖼		
B23	P ⬤	TCD O	OCDc ?	OCDs ♥						
B33	P ▢	TCD A	OCDc ?	OCDs ⬌						
B34	P ⬤	TCD A	OCDs ♥	OCDc ?	T A					
T44a	P ⬤	TCD A	OCDs ⬌	OCDc ?	T A	CT1 🖼				
T6	P ▢	TCD A	OCDs ♥	OCDc ?	T A					

Note. P = Pretraining; TCD = Two-Components-Different training; OCDc = One-Component-Different training (colour); OCDs = One-Component-Different training (shape); T = Tests; CT1 = Categorisation Training 1 (One-presentation time training); CT2 = Categorisation Training 2 (Different-presentation times training); GT = Generalisation Test.

2.5. Data Evaluation

Responses that were emitted during the first ten seconds of each trial formed the basis for all calculations. To overcome the problem of inter- and intra-individual variations in pecking behaviour, response rates were normalised. For each pigeon, the number of pecks emitted in each trial of a session was divided by the average number of pecks emitted in the whole session. In test sessions, which consisted of test and training trials, pecks emitted on test trials were excluded from calculation of the session mean. This means that the pecking rates on each trial (including test trials) were divided by the average pecking rate on training only.

To evaluate *acquisition performances* in Experiments 1 and 2, I used the index of rho (ρ) (Herrnstein et al., 1976), which is assessed from the nonparametric statistic U of the Mann-Whitney *U* test. The rho index illustrates the amount of overlap in response rates to positive and negative stimuli and varies from 0 (inverse discrimination) through 0.5 (no discrimination) to 1.0 (perfect discrimination). Namely, it gives the probability that an arbitrarily chosen positive stimulus will be ranked above an arbitrarily chosen negative stimulus. Depending on the number of cases the limits of significance for the rho-value differ. With 40 stimuli (20 positive and 20 negative), values $\geq$ .68 indicate significant discrimination (α = .05). In addition, possible differences in Experiment 1 concerning *learning speed* (number of sessions to reach criterion) and *performance* as a function of group membership were assessed by means of two-tailed Mann-Whitney *U* tests (α = .05). To compare *learning speed* across subjects in the two conditions of One-Component-Different training statistical analysis was performed using two-tailed Wilcoxon signed-ranks tests (α = .05).

Spearman rank correlations were calculated to assess possible correlations between *presentation times and performance* in Experiments 1 and 2. This non-parametric measure of correlation assesses the relationship between two variables – in this case between stimulus durations and performance (described as rho-values).

To evaluate *generalisation capabilities* of the birds in Experiment 2, the mean standardised response rates on positive and negative test stimuli were compared with each other. For that purpose I calculated the mean values of the standardised peck rates of test sessions, which were assessed in the manner described in the first paragraph of this section. Accordingly, I obtained mean standardised response rates to positive and negative training and test stimuli. I used the Mann-Whitney *U* test to compare the response rates to positive stimuli with those to negative stimuli separately for the training and the test component.

Furthermore, statistical analyses were conducted to estimate whether subjects showed a propensity to peck primarily during stimulus presentation ("*stimulus-focused*" pecking behaviour) and reduced response frequencies during display of the stimulus substitute. As presentation time of the stimulus and the substitute always added up to 10000 msecs, substitute presentation time increased as stimulus presentation time decreased. Refusal to peck at the substitute would thus affect peck rates in trials with short stimulus presentation times more strongly than in trials with long stimulus durations. To investigate this, I calculated Spearman rank correlations (with $\alpha = .05$) for the training phases of my study. Therefore, the relation between response rates emitted to positive training stimuli during the entire 10000 msecs counting time and the corresponding presentation times was assessed. Though, this was only done for stimulus durations where discrimination proved to be successful. Also, I decided to choose in an exemplary manner only one bird (B22a) for this type of analysis due to the fact that this was the only subject that took part in all experimental phases and showed the most stable performance. Consequently, only analyses of this bird's pecking behaviour were appropriate for comparisons over the whole study.

Finally, it should be borne in mind that some of the statistical analyses were calculated with rather small sample sizes. This, inevitably, affects the power of statistical tests and dictates caution in interpretations of significant effects or the lack thereof, as a consequence.

3. THE EXPERIMENTS

3.1. Pretraining

The Pretraining served as a "control phase". Above all, I wanted to habituate the subjects to the new "Rapid categorisation procedure" (RC-procedure). Furthermore, I gradually adapted the method to the pigeons' needs. This should improve the subjects' performance and included changes in the procedural parameters (e.g., increasing or reducing the stimulus substitute interval during negative trials or altering the number of pecks required to get food reward). Finally, the experimental procedure was as described in the General Procedure section. The figures were monochromatic circles (red) and squares (blue), which were embedded in a black rectangular background (resulting in a total stimulus size of 128 x 128 pixels or 4.5 cm). I created two different sizes of each form to reduce variation between members of each class to a minimum and therefore keep the classification task rather simple. The large circle and the large square had a height of 3.32 (± .40) cm on average; the small circle and the small square measured 1.88 (± .21) cm on average. Finally, four stimuli, two positives and two negatives, were presented. All stimuli used in Pretraining are illustrated in Figure 4.

Figure 4   The four stimuli presented during Pretraining. The colour names and the corresponding RGB values are given below. The stimuli are reduced in size for presentation purposes.

All eight subjects participated in Pretraining. For half of them the red circle was positive and the blue square was negative, and vice versa for the other birds (see Table 1). The ten presentation times provided within each session

were 500 msecs, 750 msecs, 1000 msecs, 1250 msecs, 1500 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs). Their order was randomised, but it was made sure that each of the four pretraining stimuli was shown once with each presentation time within a session of forty trials.

Due to frequent changes in procedural parameters no criterion of success was predefined, but pretraining was terminated as soon as a subject's discrimination performance was considered stable and reliable. With the exception of bird B33, which often refused to complete sessions and needed extensive training to acquire the discrimination, all subjects showed a steady rise in discrimination performance over the course of sessions. Overall, pretraining lasted about two months and included more than 40 sessions. But considering the absence of a criterion of mastery as well as the fact that experimental parameters were repeatedly changed in the course of pretraining, there was no sensible way of properly analysing and comparing the data obtained for the individual birds. However, this was not considered crucial anyway, as the only purpose of this phase was to familiarise the subjects with the RC-procedure and to optimise the procedural parameters for the subsequent experiments.

3.2. Experiment 1: Geometric Figures

3.2.1. Introduction

Experiment 1 was designed to serve two purposes. First, it should examine if the novel RC-procedure was appropriate for testing rapid discrimination abilities of pigeons. Second, the use of simplified, artificial stimuli provided the opportunity to control featural information. The present experiment should therefore not only shed light on the question of the minimum presentation time needed for discrimination of simple forms in general. It should also investigate possible interactions between the type/number of discriminative features and presentation time. Therefore, I

introduced two different types of stimuli, which differed in the types and amounts of discriminative features provided. *Two-Components-Different* stimuli differed in colour and shape, whereas *One-Component-Different* stimuli differed in only one of these features. To investigate possible differences in performance as a function of featural information, two training phases were carried out. *Two-Component-different training* required the pigeons to discriminate stimuli that were distinguishable by means of both colour and shape. This first training phase was supposed to provide insights into the effects of decreased presentation time on response behaviour. To determine in more detail the role of different stimulus features for rapid categorisation, the pigeons were then trained with *One-Component-Different* stimuli. There, the positive and negative stimulus differed in just one feature, either colour or shape. Therefore, two phases of *One-Component-Different training* were conducted, one examining the role of colour as distinctive feature, the other determining the role of shape. The hypothesis to be examined was that if one of these two components (colour or shape) required more inspection time than the other, performance in the two phases should suffer from reduced stimulus duration to different extents. *One-Component-Different training* was followed by two tests. The first test (*One-Presentation-Time test*) examined in more detail the effects of short presentation times by providing only one particular presentation time in every session. Regarding the fact that all preceding experimental stages involved sessions where different stimulus durations were intermixed, it seemed worth investigating whether pigeons' performance would be impaired by the use of just one single presentation time per session, particularly in case of very short stimulus durations. Namely, the latter may either overtax pigeons' picture processing abilities or cause motivational problems, or both. In either case, performance should considerably drop in sessions with very short stimulus durations as compared to sessions with longer presentation times. The results could therefore provide a basis for further tests and possible procedural changes. In the second test (*Ultrarapid test*) I introduced two new, very brief presentation times, namely 100 msecs and 250 msecs. By this I hoped to get some insight into the limits of pigeons' rapid categorisation abilities.

3.2.2. Methods

3.2.2.1. Subjects and Apparatus

The subjects and the apparatus were as described in the General Methods chapter. The number of subjects used, however, varied in the different stages of Experiment 1. In *Two-Component-different training* and in the two phases of *One-Component-Different training*, all eight subjects were employed. As turned out during training, the subjects differed in motivation and their willingness to work. Consequently, I decided to continue only with the subjects that were presumably the most promising ones regarding their training performances. Only the two "Strasser" (T44a and T6) and three of the homing pigeons (B22a, B10, and B34) were thus employed in the *One-Presentation-Time test* and in the *Ultrarapid test*.

3.2.2.2. Stimuli

The geometric stimuli were forms such as letters or circles in different plain colours. The figures provided different amounts and types of discriminative features. This means that they differed from each other either in colour and shape *(Two-Components-Different stimuli)* or in only one of these dimensions *(One-Component-Different stimuli: Component Colour* and *Component Shape)*. I created two different sizes of each geometric form.

In the individual experimental phases the following figures were employed (Figure 5). In *Two-Components-Different training* I used a stimulus set that allowed discrimination by means of both colour and shape information. This set consisted of an orange letter "A" and a purple letter "O". The stimulus set of *One-Component-Different training (colour)* provided only colour information as discriminative cue. It comprised "question marks" of different colours, maroon and aqua. The two classes of stimuli of *One-Component-Different training (shape)* were only distinguishable through their shape. I used

a heart-shaped form and a double-headed arrow, both identical in colour (silver). In the two test phases, *One-Presentation-Time test* and *Ultrarapid test*, I selected the familiar *Two-Components-Different* images as test stimuli to increase the chances of successful discrimination. This was done because on the one hand, they redundantly differed in both colour and shape and were thereby most dissimilar, and on the other hand, all birds proved to be able to discriminate them correctly. Additionally, the stimuli of *One-Component-Different training* didn't seem to be appropriate, since, to control for possible order effects, the birds were trained on the two tasks of *One-Component different training* in a counterbalanced design concerning experimental order and this fact thus led to different training schedules for the individual birds.

The large geometric forms measured on average 1.86 (± .31) cm in height, whereas the small geometric forms had a size of 1.28 (± .24) cm on average. All stimuli were embedded into a black rectangular background (resulting in a total size of 128 x 128 pixels or 4.5 cm,). Consequently, four stimuli (the large and the small positive and the large and the small negative), were presented, in each experimental phase. All stimuli used in Experiment 1 are illustrated in Figure 5.
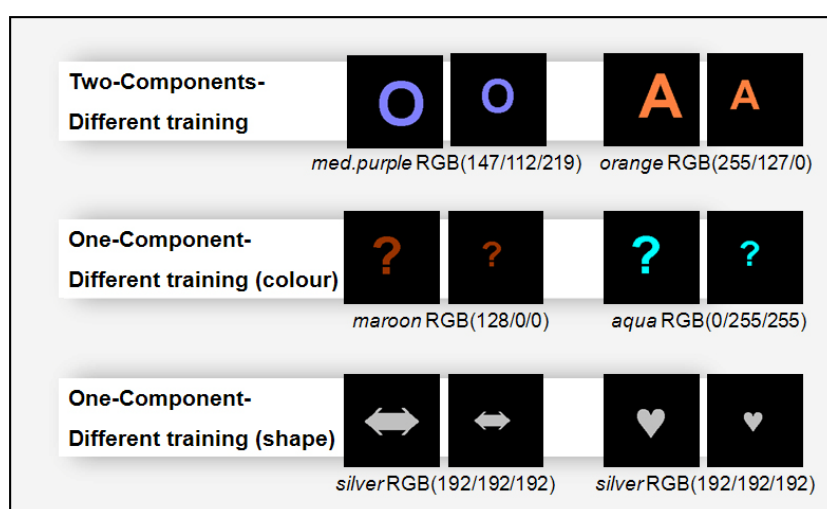
Figure 5   The 12 stimuli presented during the different experimental phases of Experiment 1. The colour names and the corresponding RGB values are given below the stimuli. The stimuli are reduced in size for presentation purposes.

3.2.2.3. Procedure

The procedure was basically as described in the General Methods chapter. Exceptions concerned the presentation times provided within each session (ranging from 100 msecs to 10000 msecs), as well as the subjects' individual training histories and reinforcement contingencies. Furthermore, there were differences concerning the number of sessions required to complete each experimental phase and thus also differences in the number of cases that eventually entered statistical analysis. Table 2 gives an overview of the complete experimental design of Experiment 1 (in case of the three training phases only description of the last three successful sessions are included).

Table 2
Overview of the experimental design of Experiment 1

Condition	Sess	Trials	PT	PT/Sess	Trials/PT
Two-Component-Different training *	3	40	10	10	12
One-Component-Different training (colour) *	3	40	10	10	12
One-Component-Different training (shape) *	3	40	10	10	12
One-Presentation-Time test	10	40	10	1	40
Ultrarapid test	10	40	5	5	80

Note. Sess = number of sessions; Trials = number of trials per session; PT = number of different presentation times; PT/Sess = number of different presentation times used per session; Trials/PT = number of trials presented per presentation time; * only the last three successful sessions are included.

Two-Components-Different training

Within each 40 trial session, each of the four stimuli was presented once with each of the ten different presentation times (500 msecs, 750 msecs, 1000 msecs, 1250 msecs, 1500 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs). The order of presentation times was randomised. The birds were required to discriminate between the "O"s and the "A"s. Stimulus contingencies were counterbalanced across subjects (see Table 1). For pigeons B33, B34, T44a and T6, the "A"s were positive and the "O"s were negative (Group A+), whereas for birds B2, B10, B22a, and B23 the "O"s were positive and the "A"s were negative (Group O+). Training was terminated when a pigeon performed three consecutive sessions in which significant discrimination was

demonstrated ($\rho \geq .80$). This criterion was beyond the rho-value indicating significance at the 5%-level (.68) and was chosen to assure excellent performance. If this criterion was not fulfilled within 60 sessions, training was stopped.

One-Component-Different training

Both phases of One-Component-Different training, namely, the *Component Colour* phase and the *Component Shape* phase, were conducted in the same manner. Within each 40 trial session, each of the four stimuli was presented once and in randomised order with each of the ten different presentation times (500 msecs, 750 msecs, 1000 msecs, 1250 msecs, 1500 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs). In the *Component Colour training* the subjects had to discriminate between "question marks" of different colours, maroon and aqua. In the *Component Shape training*, the birds had to distinguish heart-shaped forms and forms in the shape of a double-headed arrow, both identical in colour (silver). To control for possible order effects, half of the birds (B2, B10, B22 and B33) started with the *Component Colour training*, whereas the others (B22a, B34, T44a and T6) had the *Component Shape training* as first condition. Furthermore, stimulus contingencies were counterbalanced across subjects (see Table 1). For half of the birds the maroon question marks were positive and the aqua question marks were negative in the *Component Colour* condition (Group Maroon+), for the other half these contingencies were reversed (Group Aqua+). Likewise, the heart was positive and the arrow was negative for half of the subjects in the *Component Shape* condition (Group Heart+), and vice versa for the other birds (Group Arrow+). The birds were trained to discriminate positive from negative stimuli, until they reached the predefined learning criterion ($\rho \geq .80$) three times in a row. Again, this criterion was beyond the rho-value indicating significance at the 5%-level (.68) and was chosen to assure excellent performance. If a subject didn't fulfil the criterion within 60 sessions training was stopped.

One-Presentation-Time test

Prior to this test phase it was made sure that the subjects were still able to discriminate correctly between the "O"s and the "A"s of *Two-Components-Different training*. Therefore, regular training sessions were administered until the subjects performed beyond criterion in three consecutive sessions ($\rho \geq .80$). These "retraining" sessions were excluded from later analysis. In the subsequent *One- Presentation-Time test* the same stimulus presentation times were used as during training (500 msecs, 750 msecs, 1000 msecs, 1250 msecs, 1500 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs), however, they did not vary within a session. Ten test sessions were presented, with each providing only one particular presentation time — in descending order from 10000 msecs in the first session to 500 msecs in the last. Each stimulus was therefore presented ten times per presentation time. Additionally, a regular training session with mixed presentation times was inserted after each test session to allow baseline performance to recover, if necessary. These training sessions were excluded from later analysis. The five subjects had to discriminate between the *Two-Components-Different* images, namely the purple "O"s and the orange "A"s. The same reinforcement schedule as during training was applied. Stimulus contingencies were the same as during *Two-Component-Different training* (see Table 1).

Ultrarapid test

The procedure in the *Ultrarapid test* was basically the same as during training and differed from the latter only regarding presentation times. Within each test session, three familiar presentation times were used (500 msecs, 100 msecs and 4000 msecs), and, in addition two new ones (100 msecs and 250 msecs). The *Ultrarapid test* included 10 sessions. Therefore, each stimulus was shown twenty times per presentation time. The same five subjects as used in the *One-Presentation-Time test* had to discriminate between the *Two-Components-Different* images ("A"s and "O"s). Again, the stimuli were reinforced as during training. Stimulus contingencies stayed the same as in *Two-Component-Different training* for the individual subjects (see Table 1).

3.2.3. Results

Two-Components-Different training

All eight pigeons learned to discriminate between "A"s and "O"s, at criterial level. They needed 14.63 sessions on average, ranging from a minimum of five sessions (bird B2) to a maximum of 37 sessions (bird B33). Acquisition performance is shown as rho-values separately for each bird in Figure 6. There were no significant differences in learning speed (sessions needed to reach criterion) between Group A+ and Group O+ (Mann-Whitney *U*-test; z = -1.742, p = .086, two-tailed test, $_1n_2$ = 4).
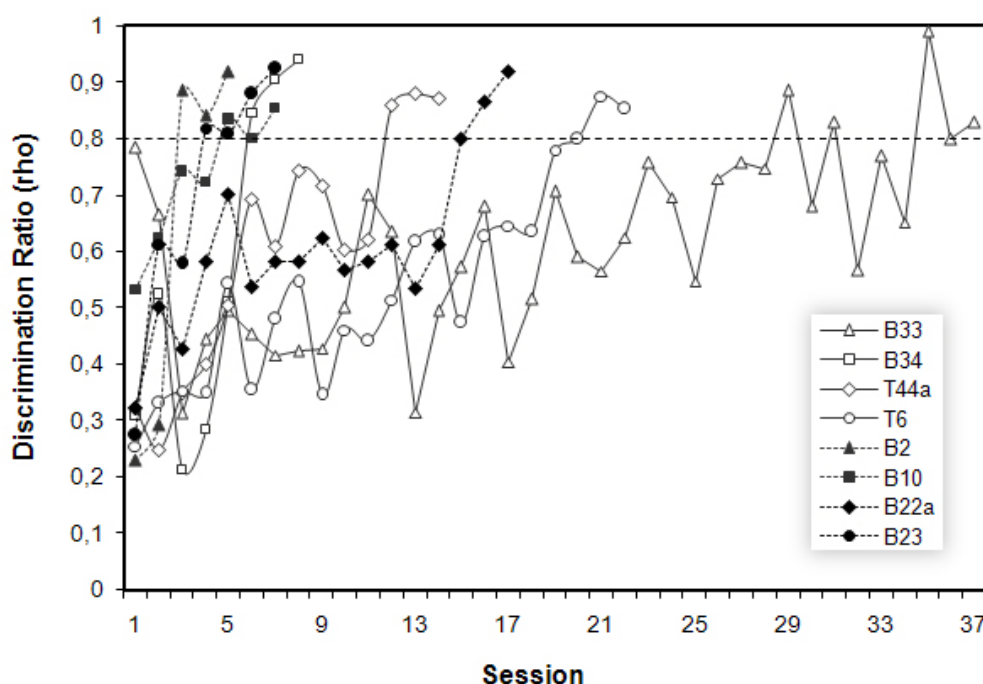
Figure 6   Acquisition curves of all subjects in the Two-Components-Different training (continuous line, open symbols: members of Group A+; dashed line, filled symbols: members of Group O+). Performance is shown as ρ-values. The dashed horizontal line indicates the chosen learning criterion (ρ ≥ .80).

Regarding examination of the individual subjects' performance, the two outliers emerged as most interesting. The fastest bird (B2) started below chance in the first session (ρ = .23), which could be due to the similar shapes of the positive stimuli shown during Pretraining (circle) and in the present training (letter "O"). Astonishingly the bird reached the level of statistically significant

discrimination in session three. This can be interpreted as a sign for the bird's flexible re-evaluation of stimuli already associated with a particular contingency. B33 is interesting owing to his extraordinarily long acquisition phase. Namely, this subject needed 37 sessions to reach criterion. B33 may have needed extended training because the circle was positive for this bird during Pretraining, but the — similar looking — "O" was negative in Experiment 1. Furthermore, it should be borne in mind that, this bird had frequently refused to complete sessions during pretraining. This suggests that bird B33 may have had general problems with getting accustomed to the new procedure. All other subjects showed a steady rise in discrimination performance over the course of sessions. There is no indication that they were influenced by the stimuli they had previously encountered during Pretraining.

It is not sufficient, however, to just examine the learning performance on whole sessions (which comprised ten different presentation times) because information about the subjects' reactions to varying time spans can't be extracted. Hence, I split up for each bird the last three sessions according to presentation time. Mann-Whitney U tests comparing peck rates on positive and negative stimuli for each presentation time were carried out for the pooled data of these three sessions ($_1n_2$ = 6, per presentation time) and ρ-values were calculated for each subject. Figure 7 shows the performance in these sessions as rho values and taken as means across all subjects (± stddev.).
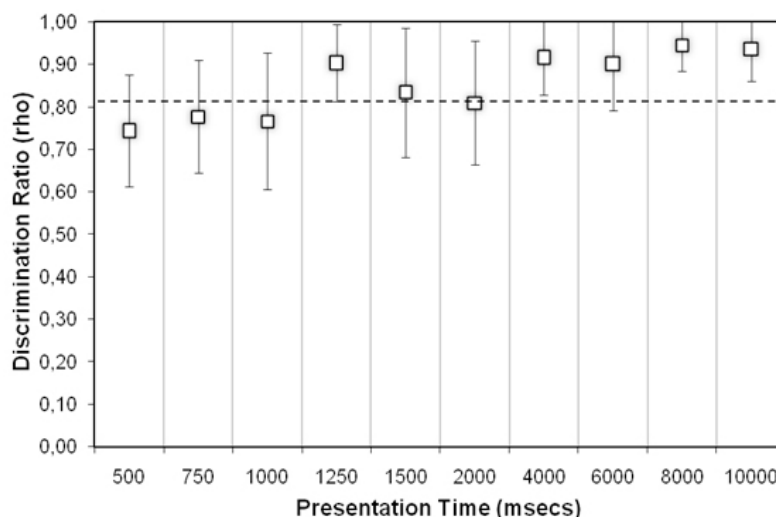
Figure 7   Performance (as ρ-values) in the last three sessions of Two-Components-Different training depicted for each presentation time (in msecs). Means were taken across the three sessions and all subjects (± stdev.). The dashed horizontal line denotes level of significance ($\rho \geq .813$, for $\alpha = .05$).

In general, performance was poorer with short than with long stimulus durations and Spearman rank correlation yielded a significant main effect of duration (r = .894, p ≤ .001, two-tailed test, $_1n_2$ = 10), indicating that the birds' overall performance deteriorated with shorter exposures to the stimulus. Times beyond 1250 msecs resulted in discrimination above criterial level ($\rho \geq .82$) — with the exception of 2000 msecs duration where the pigeons just missed the criterion ($\rho = .81$). On average, the subjects failed to discriminate stimuli shown for less than 1250 msecs beyond criterial level. At the individual level, however, response behaviour varied considerably. It is therefore inevitable to assess the subjects' individual performances. Data of the individual birds appear in Table3.

Table 3.

Average ρ-values of the last three sessions of Two-Components-Different training, shown separately for the individual birds and for the different presentation times (in msecs). ρ-values beyond criterion ($\rho \geq .813$) are given in bold face.

Subject	500 msecs	750 msecs	1000 msecs	1250 msecs	1500 msecs	2000 msecs	4000 msecs	6000 msecs	8000 msecs	10000 msecs
B2	**0.83**	**1.00**	0.76	**0.94**	**1.00**	0.74	**0.97**	**0.85**	**0.93**	**0.99**
B10	0.47	0.75	**1.00**	**0.94**	**0.92**	0.67	0.76	**1.00**	**0.97**	**0.82**
B22a	**0.86**	**0.88**	**0.82**	**0.89**	**1.00**	**1.00**	**0.86**	**0.85**	**0.83**	**0.94**
B23	**0.81**	0.58	0.75	**1.00**	**0.88**	0.68	**1.00**	**0.86**	**1.00**	**1.00**
B33	0.76	0.78	**0.82**	0.75	**0.82**	0.75	**1.00**	**1.00**	**1.00**	**0.97**
B34	0.74	**0.82**	**0.85**	0.79	0.61	0.69	**0.94**	0.69	**0.89**	**0.82**
T44a	0.64	0.79	0.44	**1.00**	**0.83**	**1.00**	**0.83**	**0.96**	**0.94**	**1.00**
T6	**0.85**	0.63	0.69	**0.92**	0.61	**0.94**	**0.97**	**1.00**	**1.00**	**0.94**

It should be borne in mind that the small number of cases to be compared (six per class and stimulus duration) makes it difficult to find any significant differences and advises caution in interpreting possible lacks of such. Nevertheless, there were some obvious trends. All subjects performed above criterion when stimuli were presented for 8000 msecs and 10000 msecs and seven out of eight were able to do so with stimuli presented for 4000 msecs and 6000 msecs. One pigeon (B22a) discriminated above criterion regardless of presentation time. Short presentation times didn't affect its performance at all (Spearman rank correlation; $r = .037$, $p = .920$, two-tailed test, $_1n_2 = 10$). Finally, half of the subjects were able to distinguish positive stimuli from negative stimuli when presented for only 500 msecs.

To evaluate the possible influence of a *stimulus-focused* pecking behaviour (i.e., preferential pecking on the stimulus but not on the substitute), a Spearman rank correlation was calculated with the data of subject B22a. For this, the response rates per trial for each presentation time, emitted to positive training stimuli were correlated with the respective presentation times ($r = -.253$, $p \leq .052$, two-tailed test, $_1n_2 = 60$). The test indicated that there was no correlation between response rates and stimulus durations, indicating that subject B22a's pecking behaviour was not significantly influenced by increasing stimulus substitute presentation time.

One-Component-Different training

Acquisition performance of the subjects was assessed separately for the two conditions (*Component Colour* and *Component Shape*) and is shown as ρ-values in the two panels of Figure 8.

A ("colour")
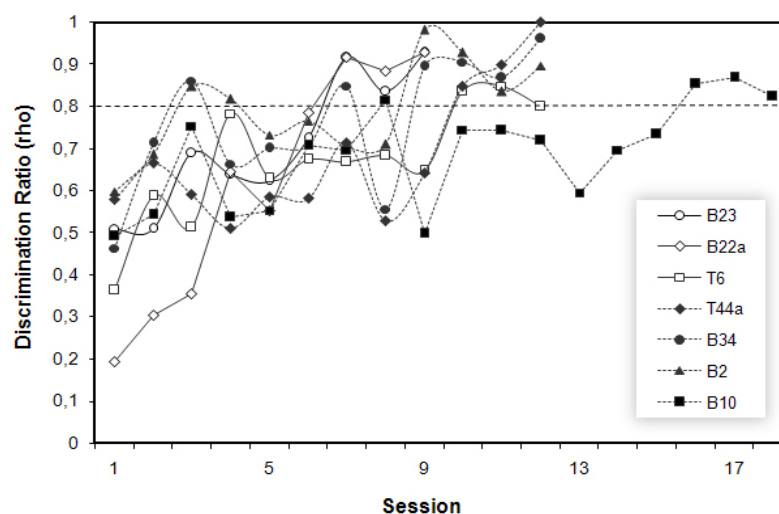
B ("shape")
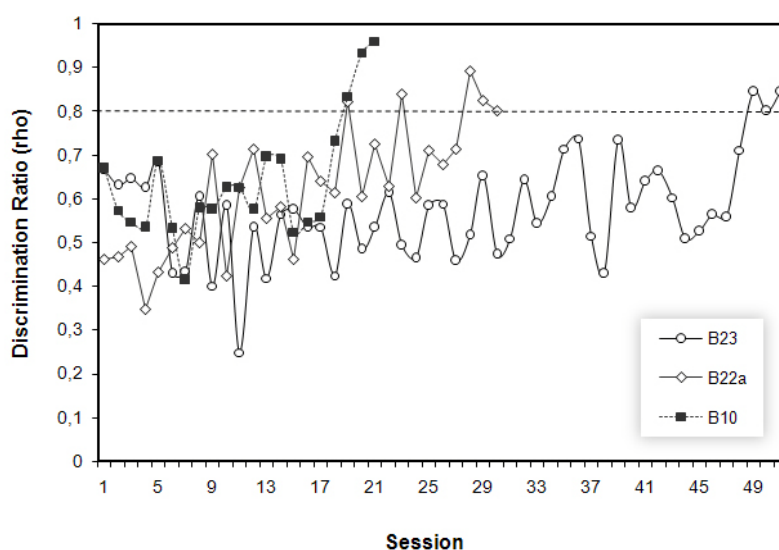
Figure 8 Acquisition curves of (A) the seven subjects that reached the learning criterion in *Component Colour training* (continuous line, open symbols: members of Group Maroon+; dashed line, filled symbols: members of Group Aqua+), and of (B) the three subjects that reached criterion in *Component Shape training* (continuous line, open symbols: members of Group Heart+; dashed line, filled symbols: members of Group Arrow+). Performance is shown as ρ-values over the course of sessions. The dashed horizontal lines indicate the chosen learning criterion ($\rho \geq .80$).

The *Component Colour* discrimination task was learned very quickly by seven of the eight subjects. The number of sessions needed to reach the learning criterion was 12.29 on average, ranging from a minimum of nine sessions (bird

B22a and bird B23) to a maximum of 18 sessions (bird B10). Only subject B33 wasn't able to meet the criterion within 60 sessions. By contrast, the *Component Shape* discrimination task caused severe problems. In this phase, only three (B10, B22a and B23) out of the original eight pigeons were able to fulfil the learning criterion within 60 sessions. This required 34 sessions on average, with a minimum of 21 sessions (bird B10) and a maximum of 51 sessions (bird B23). Accordingly, learning speed (sessions to reach criterion) of the eight birds in *Component Colour* discrimination training deviated significantly from that of *Component Shape* discrimination training (Wilcoxon signed-ranks test; z = -2.388, p = .016, two-tailed test, $_1n_2$ = 8). Failure to discriminate between stimuli of the same colour can, however, not be attributed to deficient performance particularly during short presentation times, because discrimination in the unsuccessful subjects was generally poor, irrespective of how long the stimulus was displayed.

Statistical analysis was performed using Mann-Whitney *U*-tests to assess possible differences in learning speed (sessions to reach criterion) between Group maroon+ and Group aqua+ *(Component Colour training)* and between Group heart+ and Group arrow+ *(Component Shape training)*. However, acquisition performance was not influenced by group membership in either condition (Mann-Whitney *U*-tests; *Component Colour training*: z =-.595, p = .571, two-tailed test, $_1n_2$ = 4; *Component Shape training*: z =- .189, p = 1.000, two-tailed test, $_1n_2$ = 4).

To analyse performance with different presentation times, I split up the last three sessions of each of the successful birds according to presentation time. ρ-values for each presentation time were calculated on the basis of Mann-Whitney *U* tests, which compared peck rates on positive and negative stimuli of the pooled data of these three sessions ($_1n_2$ =6, per presentation time). This was done separately for the *Component Colour* and the *Component Shape* condition. The results are illustrated as rho values in Figure 9 with means taken across subjects (±stddev.).

A ("colour")
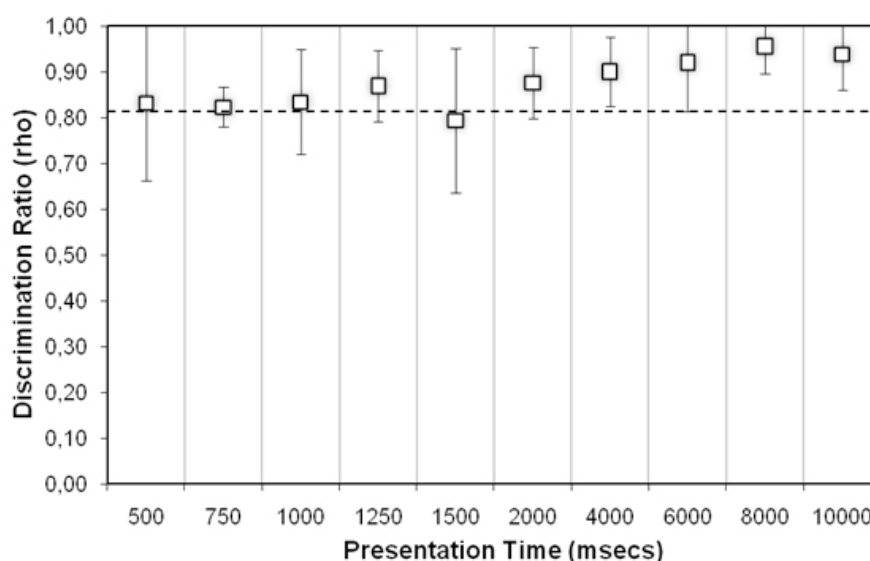
B ("shape")
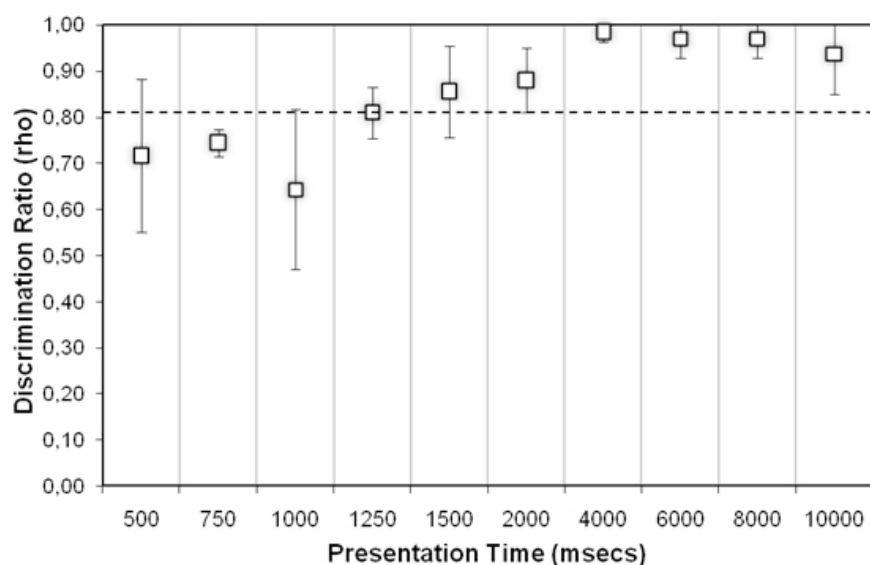
Figure 9   Performance (as ρ-values) in the last three sessions of (A) *Component Colour training* and (B) *Component Shape* training, depicted separately for each presentation time (in msecs). Means were taken across the three sessions and all successful subjects (± stdev.). The dashed horizontal lines denote the level of significance ($\rho \geq .813$, for $\alpha = 0.05$).

Averaged across all successful subjects and all presentation times, performance was almost the same with the stimuli that differed in colour (ρ-value: .87) and with those that differed in shape (ρ-value: .85). In both conditions, birds' overall performance deteriorated with shorter exposures to

the stimulus. Spearman rank correlations showed significant main effects of duration in both conditions (*Component Colour training*: r = .845, p ≤ .002, two-tailed test, $_1n_2$ = 10; *Component Shape training*: r =- . 851, p ≤ .002, two-tailed test, $_1n_2$ = 10), indicating that in both cases subjects' performance was a function of presentation time. The two conditions led, however, to clear differences in performance when stimuli were presented only briefly. As a group, the pigeons failed to show discrimination above criterion when *Component Shape* stimuli were displayed for 1500 msecs and less (mean ρ-value: .75, averaged across durations of 500 msecs, 750 msecs, 1000 msecs 1250 msecs and 1500 msecs), whereas they were, on average, well able to perform above criterion when *Component Colour* stimuli were flashed for 1500 msecs and less (mean ρ-value: .83). The results support the idea that short presentation times lead to decreases in performance. This was quite obvious in the *Component Shape* task, whereas it was only a slight tendency in the *Component Colour* task. This difference between the two conditions was confirmed by analysis with a Mann-Whitney *U* test. There, subjects' performance on stimuli shown for 1500 msecs and less was compared between the two different tasks (z = -2.553, p = .010, two-tailed test, n_1= 15, n_2 = 35). By contrast, comparison of performances when stimuli were presented 2000 msecs and longer revealed no significant difference between the two conditions (z = -.542, p = .595, two-tailed test, n_1= 15, n_2 = 35), indicating that performance was good, irrespective of which stimulus type (*Component Colour* stimuli or *Component Shape* stimuli) was shown. Furthermore, the group as a whole performed above criterion in the *Component Colour* task with all stimulus presentation times (except 1500 msecs). Failure to show good group performance with 1500 msecs might have been due to inter-individual variation as indicated by a relatively large standard deviation.

Hence, it was necessary to analyse the performance of single pigeons, as listed in Table 4.

Table 4.
Average ρ-values for the individual birds of the three last sessions of a) *Component Colour* training and b) *Component Shape training*, listed separately for the different stimulus presentation times (in msecs). ρ-values ≥ .813 are given in bold face and flag performance beyond criterion.

a) "colour"

Subject	500 msecs	750 msecs	1000 msecs	1250 msecs	1500 msecs	2000 msecs	4000 msecs	6000 msecs	8000 msecs	10000 msecs
B10	0.52	**0.88**	**1.00**	0.78	**0.84**	**0.94**	**0.83**	**0.86**	**1.00**	**0.83**
B22a	**0.92**	0.75	**0.83**	**0.90**	0.64	**0.94**	**0.86**	**1.00**	**0.94**	**1.00**
B23	**1.00**	0.79	**0.90**	**1.00**	**0.90**	**0.81**	**0.97**	0.74	**0.89**	**0.88**
B34	**0.92**	**0.85**	**0.92**	**0.82**	**0.97**	**0.88**	**0.92**	**0.85**	**1.00**	**1.00**
T44a	**0.89**	**0.82**	**0.81**	**0.83**	**0.91**	**0.92**	**1.00**	**1.00**	**1.00**	**1.00**
T6	0.68	**0.82**	0.69	**0.82**	0.75	0.72	**0.93**	**1.00**	**0.86**	**1.00**

b) "shape"

Subject	500 msecs	750 msecs	1000 msecs	1250 msecs	1500 msecs	2000 msecs	4000 msecs	6000 msecs	8000 msecs	10000 msecs
B10	0,72	0,74	0,74	**0,86**	**0,97**	**0,83**	**1,00**	**1,00**	**1,00**	**1,00**
B22a	**0.88**	0.72	0.75	0.75	**0.81**	**0.93**	**0.97**	**0.94**	**0.94**	**0.88**
B23	0.55	0.78	0.44	**0.82**	0.79	0.75	**0.92**	**0.94**	**1.00**	**0.89**

As mentioned earlier, rho-values calculated on the basis of a small number of cases to be compared (six per class and stimulus duration) have to be viewed with caution because results can possibly be misleading. Nevertheless, some trends can be identified. All pigeons were able to classify above criterion stimuli that were presented for 4000 msecs or more (with the exception of bird B23 with 6000 msecs) in both, the *Component Colour* and the *Component Shape* condition (all ρ values > .82).

In case of the *Component Colour* condition, failure at longer stimulus presentation times didn't necessarily mean failure also at shorter presentation times. Subject B23, for instance, showed perfect performance at 500 msecs (ρ-value: 1.00) but was unsuccessful at 750 msecs, 2000 msecs and 6000 msecs. One pigeon (B34) showed excellent discrimination regardless of presentation time. (Spearman rank correlation; r = .457, p = .184, two-tailed test, $_1n_2$ = 10). Finally, five out of seven subjects reached ρ-values above criterion even when stimuli were flashed for only 500 msecs.

Results were different regarding the *Component Shape* condition. First, lowering stimulus presentation time obviously affected performance and, except for one case (see below), the birds weren't able to reach ρ-values above criterion

when stimuli were presented for less than 1250 msecs. Second, taken as a group, the subjects weren't able to discriminate images presented for 500 msecs (mean ρ-value: .72). However, this was different for bird B22a. The subject performed with a rho-value of .88 when the stimuli were flashed for just the half of a second.

Again, possible detrimental effects of a *stimulus-focused* pecking behaviour were analysed with Spearman rank correlations for subject B22a. Response rates on positive trials for each presentation time where successful discrimination could be shown were correlated with the respective presentation times. This was done separately for both conditions. For the *Component Colour* condition, response rates obtained with presentation times of 500 msecs, 1000 msecs, 1250 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs, were used. For *Component Shape* condition, the included presentation times were 500 msecs, 1500 msecs, 2000 msecs, 4000 msecs, 6000 msecs, 8000 msecs and 10000 msecs. The results of both tests showed that Bird B22a's pecking behaviour was not significantly influenced by increasing presentation time of the stimulus substitute and decreasing presentation time of the stimulus (*Component Colour* condition: $r = .020$, $p \leq .894$, two-tailed test, $_1n_2 = 48$; *Component Shape* condition: $r = .288$, $p \leq .064$, two-tailed test, $_1n_2 = 42$).

One-Presentation-Time test

Performance ρ of each subject was assessed as rho-value, separately for each presentation time. Therefore, Mann-Whitney *U* tests comparing peck rates on positive and negative stimuli for each presentation time were carried out ($_1n_2 = 20$, for each presentation time). Figure 10 illustrates the results of the *One-Presentation-Time test*, with performance of the individual birds being averaged. The subjects were well able to discriminate above criterion with all presentation times. Nevertheless, progressive lowering of presentation time resulted in some discrimination decrement in absolute terms, with a Spearman rank correlation revealing a significant influence of duration on performance ($r = 879$, $p \leq .001$, two-tailed test, $_1n_2 = 10$).
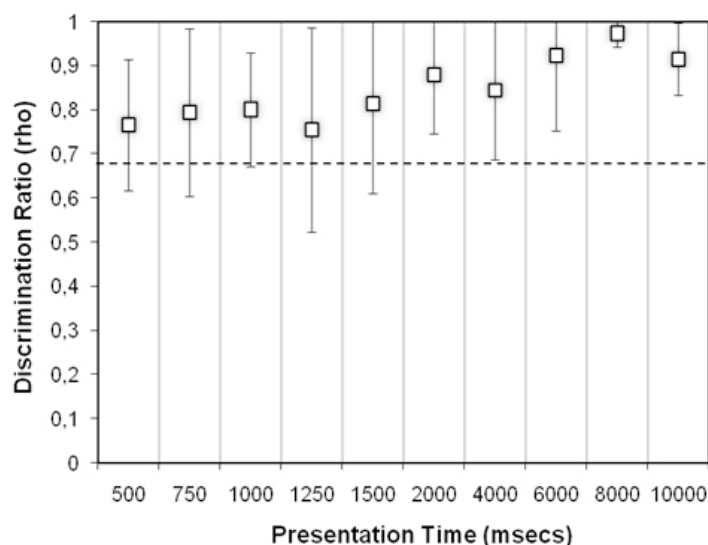
Figure 10   Performance (as ρ-values) in the ten sessions of the One-Presentation-Time test, depicted for each presentation time (in msecs). Means were taken across all stimulus presentations with each presentation time as well as across subjects (± stdev.). The dashed horizontal line denotes the level of significance ($\rho \geq .676$, for $\alpha = .05$).

I also analysed the performance of single pigeons (see Table 5). Overall, no effects (e.g., conspicuous drops in performance) of providing only one presentation time per session were obvious for most subjects, not even with very briefly shown stimuli.

Table 5.
ρ-values achieved by the individual birds in the *One-Presentation-Time* Test, shown separately for the different stimulus presentation times (in msecs). ρ-values > .676 are given in bold face and flag significant performance.

Subject	500 msecs	750 msecs	1000 msecs	1250 msecs	1500 msecs	2000 msecs	4000 msecs	6000 msecs	8000 msecs	10000 msecs
B10	0.63	0.57	**0.83**	0.62	0.49	**0.68**	0.67	0.62	**0.93**	**0.84**
B22a	**1.00**	**0.99**	**0.73**	**0.91**	**0.98**	**0.99**	**0.86**	**1.00**	**1.00**	**1.00**
B34	**0.70**	**0.87**	**0.87**	0.43	**0.88**	**0.80**	**0.70**	**1.00**	**0.96**	**0.98**
T44a	**0.68**	**0.93**	**0.95**	**1.00**	**0.97**	**0.99**	**1.00**	**1.00**	**1.00**	**0.83**
T6	**0.82**	0.62	0.62	**0.82**	**0.75**	**0.94**	**1.00**	**1.00**	**0.98**	**0.93**

Birds B22a, B34, and T44a performed significantly with all presentation times (with the exception of 1250 msecs in case of subject B34); B22a discriminated perfectly with the shortest and the three longest presentation times (and close to perfect with the others). Bird T6 was also able to classify correctly with most presentation times (including the shortest of just 500 msecs), but failed with 750 msecs and 1000 msecs. Only subject B10 performed

quite poorly throughout. This pigeon failed to reach significance in six out of the ten test sessions.

Ultrarapid test

Performance ρ of each subject was assessed as rho-values, separately for each presentation time. Therefore, the ten sessions were split up according to presentation time and Mann-Whitney *U* tests comparing peck rates on positive and negative stimuli for each presentation time were carried out with the pooled data of the ten sessions ($_1n_2$ = 40, for each presentation time). Figure 11 shows mean performances of all birds in the *Ultrarapid test*, separately for the five stimulus presentation times.
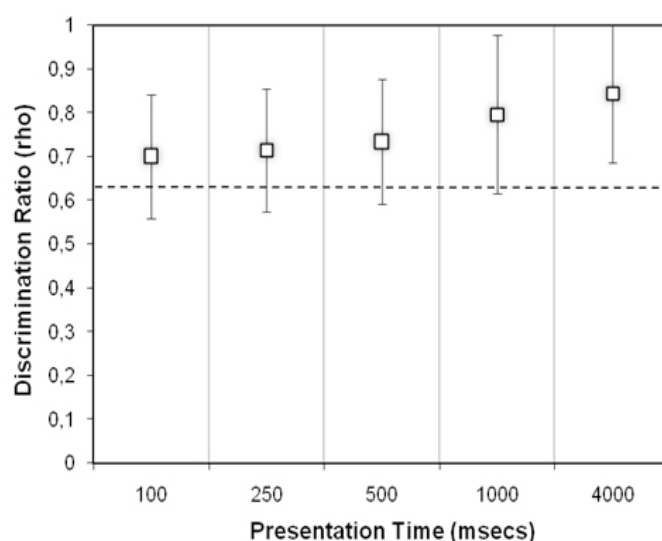
Figure 11   Performance (as ρ-values) in the ten sessions of the *Ultrarapid test*, depicted for each presentation time (in msecs). Means were taken across stimulus presentations with each presentation time as well as across all subjects (± stdev.). The dashed horizontal line denotes limit of significance ($\rho \geq$ .626, for α = 0.05).

The mean ρ-values of the whole group were significant for all presentation times, with even stimulus duration of just 100 msecs allowing for significant discrimination. But again, reduced presentation times nevertheless resulted in slightly decreased performance, and a Spearman rank correlation revealed a significant influence of duration (r = 1.00, p $\leq$ .0001, two-tailed test, $_1n_2$ =10). Table 6 illustrates the results of the individual subjects.

Table 6.
ρ-values achieved by the individual birds in the *Ultrarapid test*, shown separately for the different stimulus presentation times (in msecs). ρ-values > .626 are given in bold face and flag significant performance.

Subject	100 msecs	250 msecs	500 msecs	1000 msecs	4000 msecs
B10	0.55	0.63	0.75	0.78	0.95
B22a	0.90	0.90	0.93	0.95	0.95
B34	0.72	0.64	0.67	0.89	0.97
T44a	0.75	0.83	0.77	0.87	0.73
T6	0.58	0.58	0.54	0.49	0.62

Bird T6 failed to show significant results in the *Ultrarapid test* for any presentation time (which also explains the pronounced standard deviations in Figure 11). This could have been due to the animal's bad state of health during this experimental stage (and, indeed, it died several weeks later). The other four individuals performed significantly with all presentation times (with the exception of 100 msecs in case of B10).

To investigate in more detail why bird B10 may have failed to discriminate stimuli presented for 100 msecs, I analysed for all birds the pecks emitted during the 100 msecs of stimulus presentation. For all subjects, no more than one peck occurred during this short period. Obviously, there is not enough time for a pigeon to execute more than one peck within 100 msecs following the peck to the ready signal. Indeed, no pecks at all were emitted during stimulus presentation in the majority of trials (and most were emitted during substitute presentation). Thereby, however, it is noteworthy that B10, at least, pecked during presentation time in 12.5 % of the trials, whereas all other birds did so in only 2.5 % ± .20 of the trials. Possibly, bird B10's processing of the (only briefly flashed) stimuli was impaired by pecking during presentation and resulted in poor performance in the entire counting interval of 10 sec.

3.2.4. Discussion

There are two key findings that emerged from Experiment 1. First, pigeons are basically able to identify the properties needed for successful classification of geometric stimuli that differ in colour and shape, even if they are flashed for just the half of a second *(Two-Components-Different training).* Nevertheless, presentation time was a factor that influenced the pigeons' response behaviour and performance indeed varied as a function of stimulus duration. When presentation time was further reduced *(Ultrarapid test),* birds' performance was still remarkably good in the 100 msecs condition. Pigeons thus detected stimulus identity very rapidly. My results therefore suggest that stimulus duration of 100 msecs (or perhaps even less) is sufficient for absolute stimulus discrimination by pigeons.

Second, the pigeons mastered both training phases of *One-Component-Different training* (*Component Colour* and *Component Shape training*), however, with different ease. While the subjects learned fast and steadily in the colour discrimination task, the same birds faced severe difficulties or even failed in the shape discrimination task. The few pigeons that were successful in the latter required considerably more training to meet the learning criterion than in the colour discrimination task. Obviously, the pigeons found discrimination by colour easier than discrimination by shape. Accordingly, also the improvement of performance with increasing presentation time was particularly evident in the *Component Shape* condition. What are the main implications of these findings?

The results of the present experiment confirm those of previous studies with pigeons that used shortened stimulus presentation times (see, e.g., Brown, 1991; Cavoto & Cook, 2001; Cook et al., 1992; Diekamp et al., 2002; Guttenberger & Wasserman, 1985; Maki & Leith, 1973; Mac Donald, 1993; Wasserman et al., 2002), namely, that discrimination performance decreases with shorter stimulus durations. Although one bird (B22a) showed good discrimination in all conditions of *Two-Components-Different training* regardless how long the stimulus was presented, and one bird (B23) showed

perfect performance even at the shortest presentation time of 500 msecs *(One–Component-Different training, Component Colour)*, pigeons generally seem to profit from longer presentation times. The studies cited above showed that reducing presentation time resulted in poorer performance. It was argued in the literature that, while a bird accumulates information about the stimulus during encoding time (the term refers here specifically to perceptual processing that can occur only when the stimulus is physically present), performance suffers from shortened presentation times (e.g., Zentall et al., 1997).

Furthermore, it is noteworthy that pigeons are obviously able to discriminate stimuli with presentation times even shorter than the ones used in *Two-Components-Different training* and *One-Component-Different training*. As reported by Cavoto and Cook (2001), their subjects' accuracy was markedly reduced at duration of 250 msecs but they were still able to perform above chance level. How far reduction of presentation time can be pushed before discrimination actually breaks down, was matter of the *Ultrarapid test* of my study. Evidence in the literature about the minimal presentation time to allow discrimination is equivocal. Some findings seem to indicate that pigeons are able to detect stimulus identity very rapidly – even within the range of approximately 100 to 125 msecs (Brown, 1991; Roitblat, 1980). The present *Ultrarapid Test* confirms this. Birds' performance in the 100 msecs condition was still remarkably good. My results therefore suggest that stimulus durations of 100 msecs are sufficient for absolute stimulus discrimination by pigeons.

Hence, my results are in sharp contrast with what has been reported by Cook (1997, 2001) and others regarding time limits for pigeons' ability to make absolute stimulus identifications. There is indeed mounting evidence in the literature to suggest that pigeons may not be able to extract stimulus properties necessary for identification during presentation times of 100 msecs or less (c.f.; Cook et al. , 1992; Cook & Wixted, 1997; Lamb & Riley; 1981; Langley & Riley; 1993). How can these contradictive findings possibly be reconciled? If an animal fails to master a specific task, this may not necessarily be a problem of lacking ability. There is evidence to suggest that procedural parameters can severely affect the display of an animal's capacities. This may explain pigeons'

occasionally reported failure to discriminate stimuli presented for just around the tenth of a second. First, most of the studies cited above used a Matching-to-Sample paradigm, which substantially differs from the modified go/no-go procedure employed in the present study, where the subjects had to discriminate between successively presented positive and negative stimuli. Smith (1967) for example assumes that a simple discrimination between two stimuli is easier to learn than a matching task involving two stimuli. Second, the stimuli used in the various experiments were quite different from each other. Therefore, they may have been challenging to different degrees regarding perceptual demands and processing requirements. Third, it is hardly possible to compare the birds of different studies with respect to their training histories (e.g., subjects' previous experience and period of training with the stimuli used). These, however, could have had an influence on performance. Finally, we do not know how careful the authors of different studies were in precisely controlling methodological parameters, such as timing calibrations and stimulus presentation. It could have happened, for instance, that presentation times occasionally deviated from the durations that had actually been specified. All of this has to be taken into account when comparisons between different studies are drawn, and it remains matter of discussion, which experimental conditions may actually facilitate rapid stimulus discrimination.

However, why does the number of discriminative errors rise as presentation time decreases? Possibly, differences in motivation, attention, perception or stimulus discriminability account for that decrease. Furthermore, severely reduced presentation times may have led to a greater contribution of behavioural processes that are not under stimulus control, like guessing (Blough, 1996). Another possibility is that the pigeons had a specific problem with "sustained attention" (c.f. Maki, 1975). It is essential that a subject observes a stimulus source diligently, i.e., that it remains "vigilant". In case of briefly flashed stimuli information decays rapidly, and thus affects of sustained attention will be most pronounced for shorter stimulus presentations. In the present experiment, the necessity of keeping up focused attention during stimulus exposure may have had an effect on the performance of at least some

birds, and their occasionally observed variations in response activity could thereby be explained.

Additionally, it is not clear whether subjects might have had a basic tendency to focus their pecking responses exclusively on the stimulus. Such a *stimulus-focused* behaviour would consequently reduce responses during display of the stimulus substitute. As presentation time of the stimulus and the substitute always added up to 10000 msecs, substitute presentation time increased as stimulus presentation time decreased. Refusal to peck at the substitute would thus affect peck rates in trials with short stimulus presentation times more strongly than in trials with long stimulus durations. But regarding the fact that most subjects were quite inconsistent in their response activity, *stimulus-focused* pecking can probably not (exclusively) account for the results of Experiment 1. At least, this was definitely not the case for bird B22a as could be shown with statistical analysis.

Another factor that has to be considered is birds' eye closure during pecking. Performance could be impaired due to the pigeons' reflexively closing their eyes during the middle phase of a peck (Cook, 1992b; Hodos et al., 1976; Wohlschläger et al., 1993; Zeigler et al., 1980;). This widespread opinion has been challenged by some authors (e.g., Ostheim, 1997), who have argued that the eyelids of pigeons are not completely closed during pecking head motions but that they are narrowed to a slit. Nevertheless, it could well have happened in the present experiment that the first peck following the peck to the ready signal (the grey square) was emitted within the 100 msecs presentation time. If so, the stimulus would not have been examined with eyes completely open. This might, for example, have been the case for bird B10 with 100 msecs presentation time which was the only subject that occasionally pecked in the first 100 msecs at all.

When judging the factors that might account for this brief-stimulus durations effect, which could be based on perceptual, attentional or rather motivational factors, it is necessary to analyse the wealth of the stimuli used in more detail. Above all, it would be interesting to analyse the role of different stimulus features for rapid categorisation. The pigeons were thus trained in *One-Component-Different training* with positive and negative stimuli that

differed in just one feature, either colour or shape. The results showed that colour was, relative to shape, the primary cue that the birds used to guide their decisions. It seems, thus, that colour information is better accessible to the pigeons than the information contained in the form.

The data thereby replicated previously reported effects of better discriminability of colour displays in relation to shape displays (e.g., Cook, 1992b; 2001; Delius, 1968; Huber et al., 2000; Langley & Riley, 1993; Lea et al., 2006b; Lazareva, 2005; Troje et al., 1999 Wilkie & Masson, 1976). This prior research has shown that colour per se is a much more salient feature than shape, or, to quote Kirsch et al (2008; p. 486), "pigeons' cognitive specialisation is more geared towards seeing colours and textures instead of shapes". This is in keeping with the short acquisition time needed in the *Component Colour training* of the present experiment, compared to the extraordinarily long learning phase in the *Component Shape training* (for the same effect, c.f., Zentall et al., 1997). A study coming from our lab could also prove colour/texture precedence in pigeons. Troje et al. (1999) tested pigeons to categorise human faces according to sex. The subjects solved the task by using surface information (average intensity of images and other properties such as colour of the skin, local contrast, etc.) rather than by using shape. The pigeons chose surface properties for discrimination despite the fact that the shape contained information more useful for this task than texture.

Overall, a "short presentation time"-effect was noticeable in both tasks, but was particularly evident in the *Component Shape* condition. Although one has to be critical towards comparisons of seven subjects *(Component Colour)* on the one hand with only three pigeons *(Component Shape)* on the other hand, some conclusions may nevertheless be justified. During stimulus presentation, pigeons accumulate information about the stimulus properties that permit increasingly accurate decisions. Thereby, it seems that they are basically able to process and use shape as distinctive feature even in briefly flashed stimuli, since one subject solved the *Component Shape* task also when the stimuli were presented just for the half of a second. For the most part, however, presentation times of less than 1250 msecs apparently impair discrimination by shape, and,

though to a much lesser extent, also discrimination of stimuli that are distinguishable by colour. This is essentially in agreement with Maki et al (1976) who described differences between colour and form matching in a Matching-to-Sample task as dependent on sample duration. Namely, at short durations colour matching was better than shape matching. What can be the reasons for this colour dominance, most obvious during short stimulus durations?

Some animals respond more readily or with greater accuracy in some modalities than in others and do not give equal weight to all features. Within the visual modality pigeons appear to respond more readily to colour than to form. Obviously, there exists an "attending hierarchy" (cf. Baron, 1965) of a stimulus' dimensional information. Or, to put it differently, it is highly probable that some features (e.g., surface cues) rather than others will "pop out" and are thereby more likely to attract attention. Homogenous surface properties such as colour — an identifying feature that is present in every pixel of the object to be discriminated — possibly has a smaller "attentional load" (Blough & Blough, 1997) than other features (such as form). This is, some properties impose greater attentional demands than others and therefore delay identification more strongly.

A low position in the attending hierarchy does, however, not necessarily mean that a feature will be entirely neglected. Assumedly, this was to some extent the case during *Component Shape training*. There, at least three birds eventually mastered the task, and one (B22a) was even able to detect the relevant distinctive feature (shape) within 500 msecs (although it, surprisingly, failed with some longer presentation times). This suggests that the problem of using shape information may have been attentional rather than perceptual in nature. In the *Component Colour* condition, the "pop-out" of colour (as opposed to shape) may have alleviated the problem of lacking attention during stimulus presentation. Colour might be easier and more effortless to discriminate when presented briefly because it is largely independent of view and resolution. Shape cues, in contrast, are resolution and view dependent and it may therefore require elaborate processing to extract them from a stimulus.

To research into possible effects of vigilance and motivation related to procedural set-up, the *One-Presentation-Time test* was conducted. Very stable performance in all but one instance (subject B2) well beyond criterion and lack of a considerable drop in sessions with very short stimulus durations as compared to sessions with longer presentation times indicated that providing only one particular presentation time in each session had no negative effect on performance. Comparable levels of performance in *Two-Components-Different training* and in the *One-Presentation-Time test* suggest that the birds were quite flexible and performed without motivation deficits in case of procedural changes and adaptations. This finding may be interesting for future research using the present rapid presentation procedure.

In conclusion, Experiment 1 investigated how temporal factors may influence a pigeon's response behaviour as well as the role of different stimulus features for rapid categorisation. However, matters of interpretation are problematic, and it remains unclear which factors were actually responsible for the subjects' poorer performance with shorter presentation times. The findings are, however, based on simplified and dimensionally reduced geometrical stimuli. This raises the question whether briefly flashed images that are more complex and realistic, such as colour photographs, may be perceived, processed, and classified differently.

3.3. Experiment 2: Natural stimuli

3.3.1. Introduction

As could be shown in Experiment 1, pigeons are able to discriminate different geometric stimuli, even when they are just presented for just the tenth of a second. Hence, it seems sufficient for discrimination to catch just a short glimpse at a stimulus. Thereby, discrimination worked on the basis of simple perceptual features like colour.

But how would pigeons perform in tasks with more complex, "natural" stimuli, such as colour photographs of human beings, which can only be solved by means of a combination of features? There, no single feature is by itself necessary or sufficient for classification, but each contributed to class membership in an additive way (*"polymorphous feature rule"*; Ryle, 1951). As a consequence, class membership is not a matter of all-or-nothing in such tasks, but a matter of more-or-less. Each feature contributes incrementally to category membership. A natural category such as "person/non person" is therefore "fuzzy" or probabilistic (e.g., Medin & Smith, 1984; for reviews see Huber, 1999, 2001, and Jitsumori & Delius, 2001). By contrast, in Experiment 1 of the present study, classes could be described as being "well-defined", which means that the class-defining features were singly necessary and jointly sufficient for class membership. One may therefore expect differences in the pigeons' information processing when confronted with either an "artificial" or a "natural" categorisation task, as well as behavioural responses depending on stimulus complexity. As a consequence, brief stimulus durations may also have different detrimental effects on the discrimination of complex natural as compared to simple artificial stimuli. If so, which types of stimuli (complex or simple) would require longer presentation times for successful classification?

What almost all experiments examining categorisation of complex visual stimuli in pigeons have in common is the fact that the birds are allowed to scan and check the stimuli for at least several seconds (for an exception, see

Lazareva & Wasserman, 2009). It is not known so far whether they would perform similarly, if stimulus presentation times were considerably reduced and the pigeons were thus forced to take decisions on the basis of the first rapid pass through the visual system. To investigate this, Experiment 2 was conducted. During *One-Presentation-Time training* the pigeons had to learn to classify pictures according to the presence or absence of people. To provide a baseline for further tests, only the longest presentation time (i.e., 10000 msecs) was used in order to permit a sufficiently long time span during which the subjects could extract all the featural information needed for categorisation. After *One-Presentation-Time training*, another categorisation training phase was carried out with the same subject that was successful during the first training phase. The *Different-Presentation-Times training* investigated in more detail whether reducing presentation time would affect performance in a „person/non person"-discrimination task, when the class-defining features have been already extracted and used during the previous training phase. In order to investigate what strategy enables discrimination of the two classes, a *Generalisation test* was conducted. Regarding familiar photographs, categorisation could be achieved by learning all exemplars by rote; and some animals have been shown to possess large rote memory capacities for visual objects. Pigeons have proved to have impressive exemplar-specific memory capacities (e.g., Cook et al., 2005; Fagot & Cook, 2006). An appropriate method to evaluate whether classification is based on mere rote learning or involves some abstraction of category-relevant information is transfer testing. Thereby, a subject is confronted with novel exemplars of the two classes in a transfer test. If it is able to categorise correctly, one can infer that it has obviously extracted category-specific information (in the present task, common features of human figures). Using varying stimulus durations should help to examine the possible influence of presentation time on transfer performance.

3.3.2. Methods

3.3.2.1. Subjects and Apparatus

The subjects and the apparatus were as described in the General Methods chapter. Over the course of Experiment 1, just two of the subjects turned out to perform well enough to be continued (T44a and B22a). Hence, I decided to employ only these two in Experiment 2. As only Subject B22a passed the criterion in *One-Presentation-Time training*, only this bird proceeded to the next stages of Experiment 2 *(Different-Presentation-Times training* and *Generalisation test)*.

3.3.2.2. Stimuli

The stimuli were chosen arbitrarily from the pool of images used in the "person/non person" studies by Aust and Huber (2001, 2002, and 2003). These full colour photographs were originally taken from the database of the PHOTODISC Starter Kit and the PHOTODISC collection. They consisted of digitised bitmap files of various natural scenes. Half of them depicted one or more human beings, whereas the other half did not. The backgrounds of the person-present pictures varied, and so did the depicted person(s), namely, regarding their number, sex, size, age, angle of regard, and position in the scenery. The person-present pictures included close-up as well as long distance shots. Furthermore, orientation varied such that the person(s) in the photos faced different directions. Also the people-absent stimuli varied with respect to the appearance of the landscapes, or objects they showed. The stimuli were presented at a size of 128 x 128 pixels (45 x 45 mm) at a resolution of 28.35 pixels/cm. A total of 240 pictures, 120 of each class, were used in the experiment, with 80 of them serving as training stimuli (divided into training set 1 and training set 2) and 160 as transfer stimuli. Twenty-four of the pictures used during training (twelve of each category) are displayed in Figure 11.

Figure 12   Selection of the photographs used in Experiment 2, reduced in size for presentation purposes. The red-framed pictures are representatives of the people-present category, whereas members of the people-absent category are indicated by green frames. (Note: the colour frames were not shown to the pigeons)

3.3.2.3. Procedure

The procedure was basically as described in the General Methods chapter. However, there were differences concerning the presentation times (ranging from 100 msecs to 10000 msecs) provided within each session, as well as differences concerning session composition. Table 7 provides an overview of the complete experimental design of Experiment 2.

Table 7
Overview of the experimental design of Experiment 2

Condition	PT	PT/Sess	Train	Trans	Trans/PT	Train/Sess	Trans/Sess
One-Presentation-Time training	1	1	80	–	–	40	–
Different-Presentation-Times training	8	1	80	–	–	40	–
Generalisation test	8	1	80	160	20	30	10

Note.   PT = number of different presentation times; PT/Sess = number of presentation times used per session; Train = number of presented training stimuli; Trans = number of presented transfer stimuli; Trans/PT = number of transfer stimuli presented per presentation time; Train/Sess = number of training stimuli per session; Trans/Sess = number of transfer stimuli per session.

One-Presentation-Time training

Presentation time was 10000 msecs in every 40 trial session throughout training. The birds had to classify the colour photographs according to the

presence or absence of human beings. For T44a person-present stimuli were positive and person-absent stimuli were negative, and vice versa for B22a. Training stimuli were organised arbitrarily into two sets of 40 stimuli each. After reaching rho-values ≥ .68 three times in a row with training set 1, training set 2 was applied. The learning criterion was the same as with the first set. If a subject was unable to fulfil the criterion within 60 sessions in training set 1, I stopped its training. This happened in case of subject T44a. To test for possible reasons for failure related to procedure, this bird was then given additional training with the classic "go/no-go procedure". But as the subject failed to acquire the task within 60 sessions even under these simplified conditions it was discontinued.

Different-Presentation-Times training

Eight presentation times were used, namely 100 msecs, 250 msecs, 500 msecs, 1000 msecs, 1500 msecs, 2000 msecs, 6000 msecs, and 10000 msecs. Within each session the former training stimuli (training stimuli set 1 and set 2) were shown with only one particular presentation time, running from the longest of 10000 msecs to the shortest of 100 msecs. This changed session design which was easier to operate methodologically was introduced because *One-Presentation-Time test* (Experiment 1) could prove successfully that pigeons' performance was not impaired by the use of just one single presentation time by session, even not in case of very short stimulus durations. Subject B22a was trained to discriminate pictures showing humans from pictures that did not. As in the previous training, pictures with humans were negative and pictures without humans were positive for this bird. It was trained with each presentation time (starting with 10000 msecs) until a significant rho-value (≥ .68) was reached three times in a row. If this criterion was not fulfilled within ten sessions, I stopped the respective phase due to time constraints concerning to bring my study to the close and started training with the next presentation time. *Generalisation test* sessions were inserted after training with each presentation time (no matter if the criterion had been reached or not).

Generalisation test

In this test, transfer performance to novel instances of the two classes was examined. As test stimuli 160 novel images (80 of each class) were employed. These were interspersed into sequences of normal training stimuli at a rate of 10 per session (five of each class and session). Each transfer stimulus was presented only once. Both the transfer and the training stimuli were shown with training contingencies (i.e., they were reinforced). The same eight presentation times were used as in the *Different-Presentation-Times training*, and twenty test stimuli (ten of each class) were shown with each presentation time. This means that there were two test sessions for each presentation time. These were consecutively inserted immediately after the sessions with the same stimulus duration of the *Different-Presentation-Times test*.

3.3.3. Results

One-Presentation-Time training

Bird T44a wasn't able to learn the task and did not achieve a single rho-value ≥ .68 within 60 sessions. Furthermore, it failed on the same task in an ordinary "go/no-go procedure". Bird B22a, by contrast, learned very quickly and accurately. It needed five sessions to master set 1 and eight sessions to master set 2. The introduction of novel stimuli at the beginning of training with set 2 caused some detriment to discrimination, but performance fully recovered shortly after. The learning curves for bird B22a are illustrated in Figure 13, left panel.

Different-Presentation-Times training

Fig. 13 (right panel) shows that subject B22a's performance was strongly dependent on stimulus presentation time.
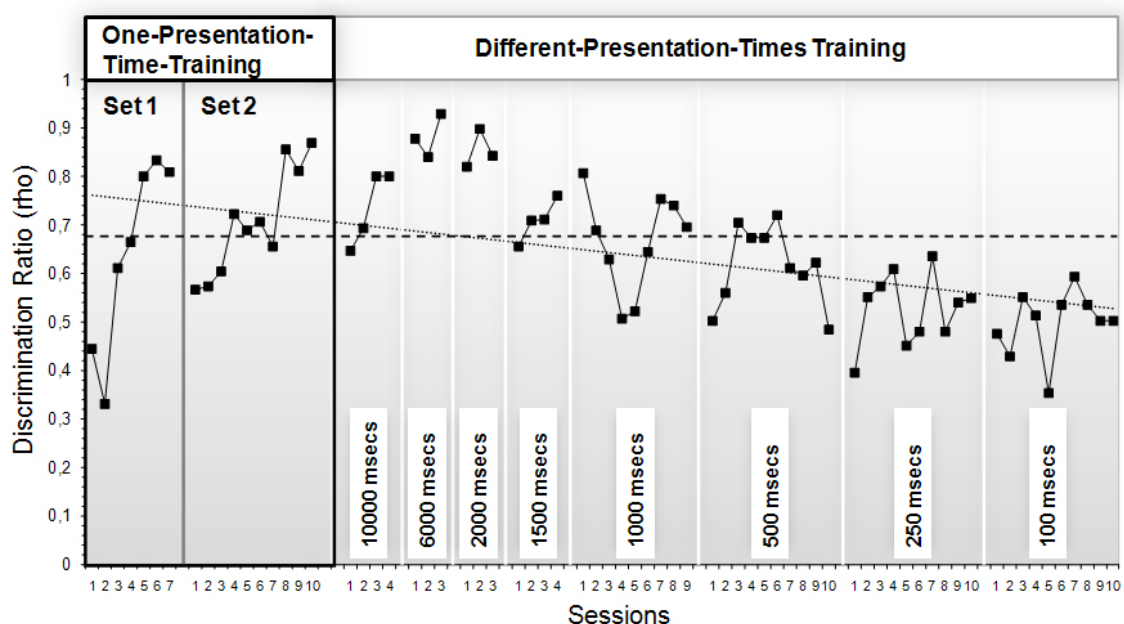
Figure 13   Acquisition performance in the training phases of Experiment 2, depicted as ρ-values on a session-by-session basis. The white vertical lines indicate the points at which generalization sessions were inserted. Decreasing performance is indicated by a dashed regression line, based on the ρ-values. The dashed horizontal line denotes the limit of significance (ρ ≥.68).

Generally, performance in *Different-Presentation-Times training* deteriorated as function of presentation time and a Spearman rank test was used to analyse this relation. Therefore, rho-values were averaged across all sessions involving the same presentation time. The test revealed a significant influence of stimulus duration on performance ($r = 929$, $p \le .001$, two-tailed test, $_1n_2 = 8$). This influence was evident not only from decreasing discrimination as presentation times became shorter, but also from the number of sessions needed to reach criterion (if the latter was met at all). Averaged across sessions, classification performance reached criterial level with 10000 msecs presentation time (N.B. the point of changing from stimulus set 1 to set 2 and the resulting temporary drop in performance; ρ-value: .74), 6000 msecs (ρ-value: .88), 2000 msecs (ρ-value: .85) and 1500 msecs, (ρ-value: .71). Reducing duration to 1000 msecs already had a clear detrimental effect, reflected by a relatively high number of sessions necessary to reach criterion (9 as compared to 3-4 for longer presentation times) and a non-significant mean rho-value (.67). Further reduction of presentation time continued this trend and further decreased performance. Discrimination was strongly affected with 500 msecs

(ρ-value: .61), and the subject failed to fulfil the criterion of mastery within ten sessions. Nevertheless, rho-values in sessions three (0.71) and six (.72) indicate that some information necessary for classification could be extracted. Bird B22a clearly performed at chance level with presentation times of 250 msecs (ρ-value: .53) and 100 msecs (ρ-value: .50) in all ten sessions.

Generalisation test

Generalisation performance of bird B22a is illustrated in Figure 14 as mean standardised response rates, shown separately for the eight presentation times and in comparison with performance on training stimuli within the respective test sessions.
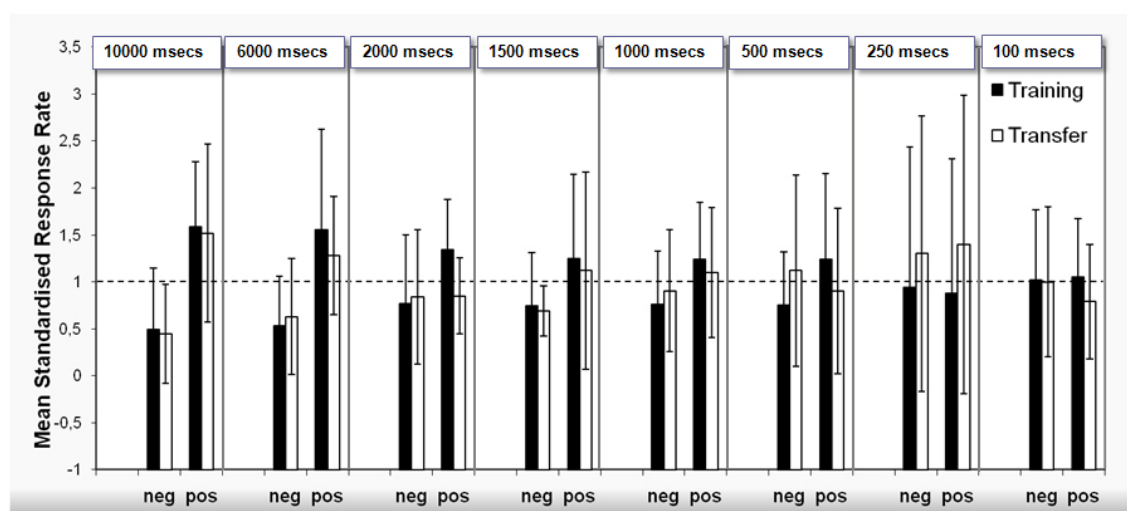
Figure 14   Transfer performance of subject B22a on the eight stimulus durations is shown as mean standardised response rates (± stdev.) for both stimulus classes (positives and negatives) and in comparison with the performance on the training stimuli of the respective sessions. The dashed horizontal line indicates the average response level (corresponding to ρ = .50)

For each presentation time, Mann-Whitney *U* tests (α = .05) were carried out to compare responses to positive and negative training stimuli as well as responses to positive and negative transfer stimuli. Therefore, data was pooled across sessions. Additionally, the corresponding rho-values were calculated. This was done for both the training component and the test component. Table 8 displays bird B22a's performance in the *Generalisation test*.

Table 8.

Results of Mann-Whitney U Tests (z-, p- and ρ-values; α = .05) assessing differences in responding to positive and negative stimuli of the training component (Training) as well as of the test component (Transfer) in the Generalisation test of Experiment 2. The results are listed separately for each Presentation Time (PT).

PT (msecs)	Training				Transfer			
	$n_{1,2}$	z	p	ρ	$n_{1,2}$	z	p	ρ
10000	30	4.93	****	**0.87**	10	-2.35	*	**0.81**
6000	30	3.95	****	**0.80**	10	-2.27	*	**0.80**
2000	30	3.75	***	**0.78**	10	-0.65		0.59
1500	30	-2.18	*	**0.65**	10	-0.38		0.67
1000	30	-2.78	**	**0.71**	10	0.76		0.60
500	30	1.98	*	**0.66**	10	1.25		0.45
250	30	0.03		0.50	10	0.52		0.57
100	30	-0.34		0.53	10	-0.57		0.43

Significance levels: * p≤ .05; ** p ≤ .01; *** p ≤ .001; **** p ≤ .0001). Significant ρ-values are shown in bold face.

The subject's responding to the training component was similar to its performance during the *Different-Presentation-Times test*. B22a showed highly significant discrimination between positive and negative training stimuli presented for 10000 msecs and for 6000 msecs (both ps≤ .0001) and still very good discrimination of training stimuli shown for 2000 msecs (p ≤ .001). Performance was still at a significant level for 1500 msecs (p≤.05), 1000 msecs (p ≤ .01) and, other than in the *Different-Presentation-Times test*, also for 500 msecs (p≤ .05). Furthermore, the bird showed transfer to novel instances, at least for longer presentation times. It discriminated significantly between positive and negative test stimuli shown for 10000 msecs (p≤.05) and 6000 msecs (p≤ .05). For shorter presentation times no significant discrimination was found (all ps≥ .05). This show s that subject B22a wasn't able to generalise the "person/non person" discrimination to unfamiliar stimuli when displayed only briefly.

Possibly, the subject's drop in performance at short stimulus presentations was due to a *stimulus-focused* pecking behaviour. To rule out the possibility that it refused to respond to the stimulus substitute following stimulus presentation, I calculated a Spearman rank correlation. The response rates on all positive trials of each presentation time for which B22a showed

successful discrimination were correlated with the respective presentation times (500 msecs, 1000 msecs, 1500 msecs, 2000 msecs, 6000 msecs and 10000 msecs). Due to the fact that B22a was only successful in case of two presentation times of transfer testing, I only analysed response rates on training trials. Analysis failed to show a correlation between response rates and stimulus durations ($r = 129$, $p \leq .085$, two-tailed test, $_1n_2 = 180$). Hence, pecking rates to positive stimuli didn't differ significantly as a function of presentation time, indicating that performance wasn't affected by refusal to peck at the stimulus substitute.

3.3.4. Discussion

The results of Experiment 2 can be summarised as follows. (1) One pigeon was able to classify pictures according to the presence or absence of humans *(One-Presentation-Time training)*. (2) Lowering of presentation time clearly had an effect on performance. Stimulus durations lasting for just 500 msecs were, in principle, still sufficient for successful discrimination, whereas reduction to 250 msecs and less caused complete failure to classify correctly *(Different-Presentation-Times training)*. (3) Novel pictures shown for 2000 msecs or longer were classified correctly and instantaneously, however, performance depended much more strongly on presentation time than had been shown for familiar training stimuli *(Generalisation test)*. In the following, the conclusions to be drawn from Experiment 2 will be considered with reference to the three experimental parts.

One–Presentation-Time training showed that one pigeon (B22a) could sort complex, natural photographs on the basis of whether or not an image contained a human being. This finding is in agreement with several experiments, done in the wake of Herrnstein and Loveland's (1964) pioneering study, all of which reported that pigeons are able to readily acquire a "person/non person" discrimination task (e.g., Aust & Huber, 2001, 2002, 2003; Greene, 1983). It is hard to tell why performance of the two subjects (T44a and B22a) differed so strongly. Whether differences in their individual

discrimination or categorisation abilities, their understanding of the task, or their states of motivation were responsible can't be answered from the present data. Due to the fact that subject T44a didn't show successful discrimination even in additional training with the classic "go/no-go procedure", failure to classify correctly doesn't seem to be related to procedure. In other words, acquisition of the task was obviously not affected by the use of a modified RC procedure that differed in some respects from the original go/no-go procedure usually employed in „person/non person"-categorisation studies.

The findings that emerged from *Different-Presentation-Times training* were the following: (1) The results obtained with the three longest presentation times (10000 msecs, 6000 msecs and 2000 msecs) reflect bird B22a's nearly perfect classification of training stimuli according to the presence or absence of persons. Hence, it seems that performance was only marginally affected by reduction of image presentation time to two seconds. (2) Further lowering of presentation time had a clear effect, however. Thereby, the results confirm the notion of pigeons' performance improving with increasing stimulus presentation time. Although this was only a tendency, also presentations lasting for just 500 msecs were, in principle, still sufficient for successful discrimination (as indicated by occasionally significant rho-values), whereas reduction to 250 msecs and less caused complete failure to classify correctly.

A variety of reasons could account for classification decrement or even failure with considerably decreased presentation times in Experiment 2. Due to the fact that subject B22a showed successful discrimination in Experiment 1, even with presentation times reduced to 100 msecs, motivational reasons or problems with sustained attention as a consequence of the employed procedure can probably be excluded. Rather, the "short-presentation-time effect" may be attributable to discriminability of the stimuli.

The outcome of the *Generalisation test* is basically in agreement with studies that found good transfer to novel stimuli according to the presence or absence of human beings (e.g., Aust & Huber, 2001; Herrnstein & Loveland, 1964; Siegel & Honig, 1970), thereby indicating that category-specific information was exploited. However, it also demonstrates that this ability is

strongly dependent on presentation time, even more strongly than was shown for training stimuli. In fact, only images presented for ten and six seconds were categorised correctly. The minimum presentation time necessary for classification of novel stimuli therefore seems to lie somewhere between two and six seconds. Lowering presentation time to even just the half of a second was, however, sufficient for reliable discrimination of familiar training stimuli.

This suggests that pigeon's perception and internal representation of familiar and novel category instances is different. Novelty effects can be ruled out as a potentially responsible factor, regarding the good transfer found for ten- and six-seconds conditions. As argued by Aust and Huber (2001, 2002, 2003), both item- and category-specific properties were stored in parallel during learning of a people/non people discrimination task. However, it seemed that subsequent classification of familiar stimuli was rather controlled by item-specific information while classification of novel stimuli was accomplished by means of category-specific information. Assuming that the same processes were at work in Experiment 2 of the present study — what outcome would have been expected for the *Generalisation test*?

Stimulus generalisation based on category-specific information would require some abstraction of the common properties of the targets (human figures) embedded in the surrounding scene. Transfer would then be based on an extrapolation to novel stimuli that possess these features, too. This would involve a "search for the target", i.e., the subject would have to successively scan the individual stimulus parts. However, the location of a possible target in the photograph is *a priori* unknown. As Theeuwes (1993) pointed out, visual search is self-terminating and subjects stop searching as soon as the target is found. Consequently, sometimes the whole display has to be checked until the subject can take a reliable decision. Therefore, focal attention is presumably necessary for the detection of targets that are defined by a conjunction of properties (human figures). Such targets would thus be found only after a serial scan (Treisman & Gelade, 1980). Data coming from pigeons' pecking behaviour in multidimensional same-different texture discriminations (Cook & Wixted, 1997) support this idea. There, the subjects were required to respond "same"

whenever all of the elements of a multi-element textured stimulus were identical in form and colour, and to respond "different" whenever a small contrasting target region was present. Pigeons generally responded quite accurately on same-trials regardless of their duration, whereas performance on different-trials systematically improved with increasing duration. This suggests that target search indeed requires additional processing time. Even stronger support comes from a study in which pigeons were trained in a successive same/different procedure (Cook et al., 2003). They consistently failed to discriminate small, centrally located, object figures in displays shown for 1000 and for 3000 msecs. Applied to my experiment, this could mean that unfamiliar images flashed for two seconds or less did presumably not provide enough encoding time to enable a pigeon to decide whether a target was present or not. Furthermore, it has to be borne in mind that the stimuli of a natural class (like "person") vary in the number and the relative weight of the category-relevant features they contain (Aust & Huber, 2002). Many features are indicative of the presence of a person but none of them is necessary to qualify an image as a target. Thus the "presetting" of the visual system cannot be as highly specific as in training and could not rely on the same features. Therefore, the subject couldn't apply a fixed search image, which would have made target detection easier and faster.

The findings of Experiment 2 are clearly different from results obtained for human and nonhuman primates who proved capable of rapid and accurate categorisation of familiar and novel natural images presented for very brief durations (e.g., Delorme et al., 2000; Fabre-Thorpe et al., 1998; Fabre-Thorpe et al., 2001). These extreme temporal constraints were even below the stimulus presentation times that I employed. Nevertheless, it seems that both humans and monkeys could perform in high-level tasks — such as looking for an animal in a natural scene — as fast and accurately as in the simplest pop-out search tasks. How may these different findings be reconciled? Evidence coming from studies that compared early visual mechanisms of humans and pigeons is ambiguous. On the one hand, some results suggest highly analogous mechanisms used for visual search and extraction of visual information extracting in pigeons and humans (e.g., Cook et al., 1996, 1997; 2002; Cook &

Blaisdell, 2006; Nielsen & Reiner, 2007; Pearce & George, 2003; Wright & Katz, 2006). On the other hand, several findings rather support the idea of disparities between humans and pigeons. Allan and Blough (1989), for example, proposed that pigeons differ from humans in their mechanisms for visual search and argued that this could reflect a basic difference in the processes underlying early vision in the two species. Hence, the pigeon's failure to discriminate between images presented for 250 msecs and less could possibly be ascribed to differences in visual perception capacities. However, this explanation seems implausible regarding the fact that pigeons are known to possess visual capabilities that are comparable (and in some respects even superior) to those of primates (see Hodos, 1993).

Alternatively, pigeons may use different features than humans in fast categorisation which facilitate rapid processing to different extents. As proposed in a variety of studies, in rapid scene and object categorisation tasks humans quickly catch the class of the image in just a single glance (e.g., Intraub 1980; Gordon, 2004; Tatler & Melcher, 2007). The nature of the mechanisms that allow for rapid recognition is currently the subject of intense debate (e.g., Delorme et al., 2004; Evans & Treisman, 2005; Fei-Fei, et al., 2007; Joubert et al., 2009; Torralba & Oliva, 2003; Walker et al., 2008). So far, most studies have indicated a global precedence effect in humans (Navon, 1977), with processing being sensitive to the overall global layout and structure of a visual scene. A consequence of global processing is the ability to rapidly and accurately extract simple image statistics, or summary information, from the displayed stimuli (Greene & Oliva, 2009). A scene gist can be extracted quickly and an object or a scene can be identified preattentively with a fair amount of confidence, whereas object details require a serial process of looking around the scene. Global features can be registered early, automatically, and in parallel across the visual field (Treisman & Gelade, 1980). In contrast, processing of distinct and locally fixed stimulus features may be serial and may therefore require more image exposure than needed to identify the image class (Gordon, 2004). Hence, getting a rough idea about general structure is often sufficient for identifying an object or a scene as member of a particular class. Similar

mechanisms seem to be at work in non-human primates. In several studies configuration of stimulus components was found to control categorisation (Schrier & Brady, 1987; Tanaka, 2001; Vogels, 1999; but see e.g., Fagot & Deruelle, 1997; Spinozzi et al., 2003 and General Discussion for proper considerations).

However, during rapid categorisation, humans and monkeys do presumably not base their decisions on the same cues as pigeons. Accumulating evidence indicates that pigeons' behaviour towards complex visual patterns is controlled by local, detailed information under conditions where humans are more likely influenced by global features (for a review, see Lea et al., 2006a). Although Goto and colleagues (2004) pointed out that it is quite unlikely that any species or individual would always be dominated either by global or local features, pigeons could at least have some bias towards using a local rather than a global style of analysis. This seems to be especially pronounced with short stimulus presentation times. Cavoto and Cook (2001) suggest that the local level may be available first in processing or may be given priority over global-level information. Hence, global/local precedence might be influenced by the duration of the stimulus presentation. Short presentation times seem to be a factor that promotes pigeons' local precedence (Goto et al., 2004). Concerning categorisation of natural images, pigeons generally seem to favour the use of item-specific, local information (Aust & Huber, 2001). In the present study, the quick change in visual input during short image exposure might have provided just enough time for a global type of analysis like the processing of general structure. A bird that preferentially relies on item-specific local details may, however, need more time to extract the relevant properties and may thus fail when presentation time is strongly reduced.

Another interesting point is that rapid categorisation research done with primates generally used abstract, *superordinate* categories and not categories at a more *basic* level. Categorisation at the basic level is generally believed to be encouraged by high within-category perceptual similarity, whereas categorisation at the superordinate level entails low within-category similarity (Rosch et al., 1978). The members of a superordinate, more abstract,

category are quite diverse and only share a few attributes (like, "animals" or "food"), whereas the members of a basic, more concrete, category are perceptually similar and share many attributes with each other (like, "human persons"). Interestingly, recent research with humans has suggested that the visual representations of superordinate categories ("animals") may be accessed first while more detailed representations (e.g. "birds" or "dogs") may require more processing time (Macé et al., 2009).However, in the present experiment I used a category at the perceptual, basic (i. e., less abstract) level, namely "human *vs* non-human". In a comparative study with humans, monkeys and pigeons, Roberts and Mazmanian (1988) could show impressively that pigeons had no problem solving a discrimination task at the concrete level ("kingfishers *vs* other birds"), but were massively challenged or even failed when the task was more abstract ("animals *vs* non-animals"). Obviously, the reason for this was that kingfishers are perceptually similar to each other. The abstract task, by contrast, went beyond the level of evaluating physical similarities and could not be solved that easily by means of any perceptually salient, class-defining features. In my study, members of the "person/non person" concept obviously have quite a number of features in common (e.g., "human heads", "human noses", "human hands"), which might have geared the use of feature-specific search strategies and attending to "constant patterns" that appeared in all person-stimuli used. Therefore, concerning pigeons, a rapid "person/non person" categorisation task might be superior to a rapid superordinate-level categorisation. It would, though, be very interesting to know how pigeons may perform in a more abstract rapid discrimination task where common features of the classes to be discriminated are not that easy to specify (e.g., in case of "animal *vs* non-animal": "paws", "wings" or "hooves"). Indeed, there is evidence to suggest that, concerning pigeons, categorisations at different levels of abstraction are influenced by presentation time to different extents (Lazareva & Wasserman, 2009).

But for now, all we can say is that Experiment 2 of the present study implies that pigeons may be very different from primates in the means they use to solve in rapid categorisation tasks.

Apart from the problem of examining datasets obtained from just one single subject, another factor's impact on performance should not be underestimated, namely, reinforcement contingencies. Due to counterbalancing reinforcement contingencies for the two subjects originally assigned for Experiment 2, bird B22a was rewarded on person-absent pictures. Pigeons sometimes demonstrate an asymmetry in their ability to learn a discrimination task based on the presence of a target in one class and its absence from the other class. Usually, the discrimination is learned more rapidly if reward is associated with images containing the target and nonreward with displays lacking a target. Jenkins and Sainsbury (1970) labelled this asymmetry in discrimination learning the "feature-positive effect", and it has been demonstrated in numerous other studies (see, e.g., Allen & Blough, 1989; Aust & Huber, 2001, 2002; Dittrich & Lea, 1993; Edwards & Honig, 1987; Pace et al., 1980). Additionally, it was found that pigeons tend to focus their pecks on the diagnostic features of a category (e.g., Dittrich et al., 2009). In case of bird B22a, pecking was required during presentation of person-absent stimuli. This means that in negative trials it had to suppress its natural bias to peck on the target-defining features, but was required to peck in positive trials where no target features were present. Additional complication of the task by putting the subject under "time pressure" with brief stimulus presentations may then have resulted in further decrements in accuracy.

It remains to be seen to what extent the present results can be generalised and if they are evidence of a principle phenomenon in pigeons. My experiment is, to my knowledge, the first one that applied complex natural stimuli in a rapid categorisation task with pigeons. Therefore, comparisons are lacking which would help to evaluate and appropriately judge the results of bird B22a. In summary, however, they suggest at least that pigeons are basically able to discriminate and categorise natural photographs presented rapidly, despite detrimental effects of very brief stimulus durations, which most pronounced with novel, unfamiliar photographs.

4. GENERAL DISCUSSION

Decades of research have impressively shown that the pigeon is highly adept in discriminating, categorising and generalising a huge variety of different visual stimulus classes, ranging from artificial and simplified geometric forms to complex natural stimuli. However, it is still equivocal how quickly a pigeon can extract the necessary pictorial information that appears to control its discriminative behaviour. Hence, the primary goal of my study was to determine how variations in the duration of stimuli differing in complexity would affect subjects' performance. At the same time, I wanted to examine the efficiency of the Rapid Categorisation paradigm by studying pigeons' responding in a variety of tasks but with the same procedural parameters. To accomplish this, I conducted two experiments.

Generally, the employed methodology was shown to be appropriate and effective in the study of pigeons' rapid discrimination and categorisation abilities despite various modifications that were introduced throughout the study. Additionally, the two experiments of the present study have shown that pigeons do indeed benefit from increased presentation times, but also that the extent of this effect strongly depends on stimulus complexity. Data suggest that classification of natural stimuli requires longer presentation times and is thus more prone to failure with very short presentations than are discriminations of simple geometric stimuli. In the following I will consider possible reasons for this difference in classification decrement.

First, there are generally two types of mechanisms that determine performance during stimulus presentation. In *bottom-up processes*, all influences on response behaviour result directly from stimulus-driven factors. These processes are thought to operate on raw sensory input and to be based on stimulus variables such as stimulus quality and complexity. They result in a rapid and involuntary shift of attention to salient visual features of potential importance ("something attracts interest"). In *top-down processes*, by contrast, all influences on performance result from goal-driven cognitive strategies, such

as biased attention ("to know what you are looking for") or memory processing, where behaviour is voluntarily guided across various stimulus situations (Blough and Blough, 1997; Connor et al., 2004). Usually, both the properties of the image as well as the observer's expectations and goals determine detection of the relevant features. Which of these will be more likely to control behaviour depends on the demands of the specific task.

In Experiment 1 of the present study the stimuli could be identified by a single distinctive feature (colour or shape) and thereby processed via a fast, primary preattentive process, driven by low-level perceptual characteristics (e.g., Bergen & Julesz, 1983; Treisman & Gelade, 1980; Pearce & George, 2003). Therefore, discrimination in this task may have been mainly under the control of bottom-up processes. The complex natural stimuli presented in Experiment 2 may, by contrast, have required attentive processing which involved moving a "mental spotlight" from location to location. Therefore, top-down processes may have prevailed in this task. Actually, the pigeon had to attend to a huge amount of properties of the target "human figure" (Aust & Huber, 2001), and had to use differently weighted target features in order to apply a polymorphous class rule where no single, isolated feature was necessary or sufficient (Aust & Huber, 2002). Therefore, attention was presumably focused on parts of the visual field in sequence, thus leading to serial processing of one item and one location at a time.

Lea et al. (2006b) put forward the same idea, namely, that tasks that require attention to multiple dimensions are routinely found to be more difficult, or to require longer exposure, than corresponding single-dimension tasks (see also, e.g., Cook, 2001; Cook et al., 1996,). Following this line of argument, the overall pattern emerging from the various parts of the present study suggests that the speed at which the relevant features are identified varies considerably in pigeons. Under certain conditions detection and discrimination can be very rapid and maybe even parallel in nature (e.g., Hollard & Delius, 1982). This was particularly pronounced with colour being the distinctive feature in Experiment 1. In other situations, processing is much slower and serial-like in character, as was probably the case in Experiment 2, and, there,

particularly evident with novel, unfamiliar images. Presentation times between 250 msecs and 500 msecs for familiar natural stimuli and of 2000 msec or less for new stimuli might not provide enough encoding time in a complex categorisation task, whereas short presentation times may be sufficient in a simple, low-level cue discrimination task.

A *second* and closely related reason why longer presentation times were more crucial with the complex natural stimuli of Experiment 2 than with the simple geometric forms of Experiment 1 is based on the limited capacity of pigeons' input channel (c.f.: Lamb, 1991). If capacity is taxed, either by restricting encoding time or by increasing the amount of relevant information to be encoded, performance suffers ("shared attention"; "information overload hypothesis", e.g., Maki & Leith, 1973). Although this effect has been observed mainly in Matching-to-Sample tasks, it is not so far off to assume that similar mechanisms might have worked in the tasks of the present study. Namely, restricted encoding time may have decreased discrimination performance in both experiments, and this effect was even further enhanced in Experiment 2, where more information had to be processed.

Third, differences between Experiment 1 and Experiment 2 could have been based on differences in stimulus predictability. Total predictability is assumed to speed up visual processing (Delorme et al., 2004). Operations that seem to direct attention, ("priming events"; Blough & Blough, 1997), for instance through target repetition, can facilitate detection by carrying over information to the next trials in the form of a sensory trace. Repeated exposures induce a temporary perceptual readiness or attentional state which enables the searcher to detect the target more rapidly (Blough, 1992). The assumption that repeated encounters with a given target trigger a focused attentional mode is captured in a model of visual search ("attention threshold hypothesis") proposed by Bond (1983).

In Experiment 1, repeated exposures (and thus reinforcements) may have enhanced the pigeons' focus on particular simple target features (i.e., a particular colour or shape). This led them to apply some kind of search image which allowed the relevant features to be seen more readily. Being fully

informed about the target and its features should furthermore allow subjects to maximize the use of top-down strategies. In Experiment 2, the multitude of different images depicting persons of varying number and appearance would have ruled out the use of an exact 1:1 search image. As a consequence, more search time would have been needed to detect the relevant properties. In other words, few identical stimuli that were frequently repeated were shown in Experiment 1, whereas many different stimuli were shown with few repetitions in Experiment 2. This should have resulted in high stimulus predictability in Experiment 1, but not in Experiment 2. As a consequence, an exact, invariable search image could have been formed and applied in the former, but not in the latter. This, in turn, could have been the reason for the difference in performance both between Experiments 1 and 2, and between training and transfer in Experiment 2.

Moreover, the difference between experiments was possibly further enhanced by the order in which they were carried out. Pigeons are known to be rather inflexible to give up a formerly successful strategy, even if the demands of the task have changed (Aust & Huber, 2008). In the present study, bird B22a might have tried to form and apply an exact, fixed search image in Experiment 2, as this strategy had been successful in Experiment 1. But for the reasons just outlined, this was doomed to failure in Experiment 2. Apart from this, the general ease with which a search image is formed seems to depend on stimulus complexity. Langley and co-workers (1996) for example assume a tendency in pigeons to focus attention on simple features, such as colour or shape, in building up search images. Furthermore, the need for relatively long stimulus exposures when novel "person/non person" images had to be classified was possibly rooted to some extent in an inability to form an exact search image as a consequence of stimulus complexity and variability.

Fourth, with short presentation times, the subjects were required to peck in go-trials and to refrain from pecking in no-go trials in the absence of the stimulus during most of the counting time, which posed demands on their working memory. Studies investigating short-term memory in pigeons basically showed that performance accuracy declines as the delay interval increases (e.g.,

Blough, 1959). Particularly, pigeons were found to be more likely to forget the stimulus in delayed than in non-delayed Matching-to-Sample tasks. In other words, memory retention is a positive function of stimulus duration (Nelson & Wasserman, 1987; Shimp & Moffitt, 1977). When discriminations are relatively easy and retrospective demands are low and require less detailed representations (for instance in experiments using single or few-dimension stimuli, such as Experiment 1 of my study), forgetting is considered to play a less important role than in higher-level classification tasks (Roitblat, 1980; Guttenberger & Wasserman, 1985; Weavers et al., 1998; Urcuioli et al., 1999; Diekamp et al., 2002; Sargisson & White, 2001, 2003). Discrimination of complex stimuli may be harder to retain than simple low-level discriminations and may therefore be more susceptible to forgetting. Since, to my knowledge, the literature only entails studies that analysed working memory and forgetting functions in pigeons when being presented complex natural photographs for 500 msecs and more (Cook & Blaisdell, 2006; Lazareva & Wasserman, 2009), it is difficult to judge the extent to which information retention might have declined in the present experiment when presentation times were 500 msecs or less. It seems, however, that, in pigeons, forgetting of working memory contents occurs no earlier than after some seconds. It is thus quite unlikely that my subject's failure to classify correctly with presentation times of 250 msecs and less was entirely due to misremembering.

It has to be pointed out that the results obtained in the present experiment with pigeons may not be general to other species. As discussed previously, it seems that humans and monkeys base their decisions in a fast visual categorisation task, at least in part, on the same cues and on overlapping abstract representations (Fabre-Thorpe, 2003). But is the same true for pigeons or is rapid categorisation based on dissimilar processes in birds and primates, and, if so, which are the crucial differences? First, the simple task of Experiment 1 yielded discrimination with presentation times even as short as the tenth of a second. But nevertheless, performance was clearly better with longer presentation times. Such a pronounced effect of presentation time has, however, not been found for monkeys and humans (D'Amato & Worsham, 1972; Intraub,

1980; Potter, 1976; Roberts & Kraemer, 1981). Second, discrimination of even briefly flashed low-level feature displays by pigeons was found to be still quite good in the present study, whereas extended visual processing was necessary to classify complex natural stimuli. Here, a major difference between primates and pigeons is apparent (e.g., Fabre-Thorpe et al., 1998; Thorpe et al., 1996). In many situations, pigeons' relative response to different visual stimuli cannot reliably be predicted from the typical primate response to the same stimuli. It seems that, in general, visual scenes are not parsed in the same way by primates and pigeons (Lea et al., 2006b). The features that are salient within a visual scene for the former may not be equally salient for the latter. It has already been suggested that pigeons could be more prone to use a local, rather than a global, style of analysis of visual scenes (e.g., Vallortigara, 2004), whereas primates would rather show a global style of analysis (e.g., Navon, 1977). This would enable primates to use just the gist of a scene to predict the presence of an object (e.g., a human being) and possibly to even use abstract mental representations that are not accessible consciously (Fabre-Thorpe, 2003). However, findings in the literature regarding a "global precedence effect" in primates are hotly debated. Some studies addressed the issue whether or not nonhuman primates may analyse local features prior to integrating global configuration (see, e.g., Fagot & Deruelle, 1997; Spinozzi et al., 2003). But these studies were mainly conducted with simplified geometric hierarchical stimuli and it is thus problematic to apply the conclusions contained therein to studies that involved natural scenes and categories.

Generally, one must be cautious when making comparisons between species. The outlined differences may be attributed to the specialised structure and functions of the avian visual system. For example, pigeons' local precedence could be related to the fact that they have two specialised areas, or foveae, which may have different functions (cf. Hodos, 1993; see Cook, 2001). The two areas project differentially within the visual system (Remy & Güntürkün 1991), and, to some extent, information from the separate visual fields is processed independently (Remy & Emmerton 1991). The frontal visual field seems to be specialised for foraging on the ground, whereas the lateral visual field seems to

be specialised for predator detection and flight control. Moreover, Maldonado et al. (1988) showed that perception of static or slowly moving stimuli pigeons have adopted a frontal gaze that stabilises the image on the retina, whereas for fast-moving stimuli they have adopted a lateral gaze that allows the image to move across the retina. Fast moving stimuli and briefly flashed stimuli probably share some similarities. First, in both cases visual input stimulates parts of the retina with a rapidly changing spatiotemporal pattern. Second, the transient visual changes (abrupt stimulus onsets and abrupt offsets) that both types of stimuli have in common automatically attract attention through visual "pop-out". Consequently, pigeon's lateral viewing might not only be geared to and specialised for fast processing of rapidly moving objects, but also of briefly flashed stimuli. These findings are relevant to the results of the present study, because a rapid categorisation procedure presumably supports frontal viewing. This, in turn, may have favoured examination of fine stimulus details and may thus have led to mainly local processing as well as to attenuated detection of rapid stimulus presentations. Hence, further studies with the same stimuli being briefly presented to the birds' lateral visual field would be highly informative.

Finally, how can we interpret the results of the present study within an ecological context? The pigeon — as all animals — is adapted to life in its particular ecological niche. The ability to analyse the visual environment rapidly is undoubtedly an important feature of visual systems, as survival of an animal is likely to depend on the speed with which predators or food can be detected. Hence, it is quite likely that evolutionary pressure has encouraged the development of mechanisms that facilitate rapid perception and discrimination of objects. In Experiment 1, I found evidence that briefly flashed stimuli can be identified. Experiment 2 showed, however, that there are limits to this, set by stimulus complexity and demands of the task. But from an ecological point of view the ability to categorise stimuli of biological relevance instantaneously seems to be essential, and thus one has to be very careful with interpretations of the present findings. The absence of proof is, however, not proof of absence, and, as Lea and colleagues (2006a; p. 254) emphasised, "*stimuli come first, and*

if we are to understand animal cognition, we will have to understand the stimuli that we present to our animal subjects". In other words, the stimuli used in Experiment 2 obviously didn't signalise high biological relevance to the bird.

It is still a matter of debate in which way a pigeon actually perceives a photograph. Concerning pictures with and without human figures, two studies by Aust & Huber (2006, 2009) suggested that pigeons are even able to recognise the pictures' representational content. Nevertheless, it is unclear whether they indeed extract the same information from photographs and organise it in the same way as the information they extract from a briefly viewed natural scene in everyday life. It remains to be explored whether a pigeon's response to an image, which is always an abstraction of the real world, is in some way comparable to its response to the real stimulus in nature. Actually, it is quite likely that under natural conditions, which provide the possibility of three-dimensional perception and of gaze shifts from the frontal to the lateral visual field pigeons would perform differently than in the present study.

In conclusion, it should be noted that several methodological problems weaken the heuristic value of this study. (1) The data of Experiment 2 were collected from only one subject, and it is obviously difficult to draw firm conclusions from a single test animal. This demands caution in interpreting the results, and, with an *N* of one, it would clearly not be justified to attribute any effects found in Experiment 2 to a general characteristic of the species. At best, some trends and basic abilities may be inferred. (2) Furthermore, due to this subject's being rewarded on person-absent pictures, a feature-negative effect, meaning that discrimination was impeded when instances containing the target were presented on non-rewarded trials (Jenkins & Sainsbury, 1970) might have been at work and may have affected performance. (3) Due to technical constraints I implemented only a few stimulus presentation times. Therefore, the latter were reduced in quite large (and unequal) steps. It may have been more informative, however, to apply a finer grading of durations, especially in the case of *Generalisation Tests*, where the huge time gap between two and six seconds made it impossible to identify the point at which discrimination

actually started to break down. (4) As target size has been found to play an important role in visual discrimination tasks (Aust & Huber, 2002; VanRullen & Thorpe, 2001), it is possible that enlarging the images would have had beneficial effects on performance. (5) Although the Rapid Categorisation paradigm employed in the present study proved to be appropriate for studying birds' rapid classification abilities, it could well be that other experimental procedures (like a Symbolic Matching-to-Sample task) may be better suited. On the one hand, a successive go/no-go procedure as used in the present study has well-established benefits like allowing for graded responses that may be more sensitive to small changes in associative strength than a discrete choice measure. On the other hand, the possibility to choose immediately after presentation of the stimulus as can be provided by Matching-to-Sample procedures may prevent possible effects of misremembering. Additionally, possible detrimental effects on performance caused by *stimulus-focused* pecking could then be confidently excluded.

To come full circle and back to Emerson's quotation cited in the beginning — how far will a pigeon get with its first spontaneous glance? It seems that pigeons are well able to make fast — maybe preattentive — decisions on the basis of the first rapid pass through the visual system. However, this ability seems to be strongly dependent on the exact experimental circumstances. The research reported here addressed the nature and the impact of these circumstances. The results therefore have important implications for our understanding of how fast pigeons perceive and group the objects encountered in their world into categories. Although the present study did not exhaust the conditions under which rapid discrimination and categorisation of briefly flashed stimuli occur, it can, at least, serve as a starting point for a more detailed investigation of the mechanisms underlying rapid perception and processing of visual stimuli by pigeons.

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DECLARATION

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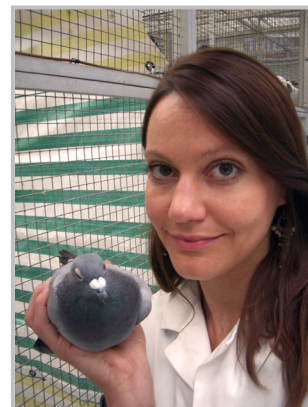
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