

Pigeons integrate past knowledge across sensory modalities

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

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Several vertebrate species have been shown to denote external events in their vocalizations and previous studies have revealed sophisticated inferring abilities in receivers that go beyond mere associative processes (reviewed in e.g. Evans 2002; Seyfarth et al. 2010; Fitch & Zuberbühler, in press). The encoded referents of such signals may range from broad to very specific contexts and seem to induce mental representations of the external events eliciting them. For instance, rhesus monkeys, *Macaca mulatta*, seem to differentiate food call types by their external referents rather than by their acoustic features (Hauser 1998), chickens, *Gallus gallus domesticus*, seem to take past knowledge into account during foraging (Evans & Evans 2007) and several alarm-calling species extract information from both the signal itself and the context in which it is uttered (Rainey et al. 2004; Ridley et al. 2007). Hence, receivers do not have an automatically triggered behavioural response but seem to take contextual knowledge into account. These sophisticated cognitive abilities have been reported for species that show both sides of information transmission: signalling and receiving (Arnold & Zuberbühler 2008; Ouattara et al. 2009a, b). However, there is by no means a representational parity between signalling and receiving, nor is 'meaning' in a linguistic sense transmitted between signaller and receiver (Fitch & Zuberbühler, in press). How different the cognitive requirements of signallers and receivers might be is

especially apparent in the alarm-calling behaviour of many species. 'Functionally referential' signals are often produced in threatening situations and are thought to decrease the level of uncertainty about a nearby threat in receivers (Seyfarth et al. 2010). They are highly context specific, show an unambiguous physical structure and trigger the same response in receivers as the actual event (e.g. Marler et al. 1992). However, while there is debate about whether the signaller intends to inform (Cheney & Seyfarth 1990; Cheney et al. 1996; Tomasello & Call 1997; Rendall et al. 2000) and about the exact definition of the information content (Rendall et al. 2009), there is growing evidence for elaborate inferring mechanisms in receivers (Fischer 1988; Rendall et al. 1996; Zuberbühler et al. 1999).

Most studies so far have focused on animal species that produce alarm calls in the context of predation and thus possess cognitive abilities that are involved in both signalling and perceiving information about predator presence. There is evidence that also some nonalarm-calling species such as lacertid lizards, *Oplurus cuvieri* (Ito & Mori 2010), iguanian lizards, *Amblyrhynchus cristatus* (Vitousek et al. 2007) and dik-diks, *Madoqua guentheri* (Lea et al. 2008) associate heterospecific vocal cues with predator presence and that they eavesdrop on these signals to avoid predation. However, whether nonalarm-calling species are also able to decode the referent of the signal and to infer the event that elicited it remains unknown. In general, nonalarm-calling species may provide a promising basis to address questions concerning cognitive mechanisms that underpin call interpretation in highly vocal species. Specifically, we can test whether advanced interpretation mechanisms found in alarm-calling species are specialized cognitive

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abilities that are used for communication or whether they represent more general inferring abilities that are not domain specific.

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

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

METHODS

Subjects and Housing

We tested 60 adult pigeons in pairs ($N = 30$) from March to June 2011. All birds were colour-ringed and individually identified. The pigeons were housed in flocks of 8–16 individuals in outdoor

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

Stimuli

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

Acoustic stimuli were obtained from an online source (<http://www.xeno-canto.org>) and identified as uttered in territorial behaviour. We used territory calls of two different buzzards and two different pheasants and presented them alternately to the different dyads of a group to reduce the effect of pseudoreplication. A single buzzard call lasted approximately 0.7 s and was naturally produced in a sequence of three subsequent calls, resulting in an overall duration of about 5 s (including breaks of approximately 1.4 s each). The pheasant's call lasted 0.3 s and was not naturally produced in a sequence. We repeated pheasant calls three times (including breaks of 1 s) and created sequences of about 3.5 s to expose the birds to a similar number of calls (for examples of spectrograms of acoustic stimuli see Fig. A1 in the Appendix). We did not manipulate the length of single territory calls as these reflect natural variation and provide perceptual features that may enable pigeons to discriminate between a predator and a non-predatory stimulus. To modify sequence length we used PRAAT DSP package v. 5.1.29 (Boersma & Weenink 2011). All playbacks were broadcast using an iPod Nano (fifth generation) connected to a speaker amplifier (ION Block Rocker, 70 Hz–50 kHz ± 3 dB).

Behavioural Variables and Data Analysis

We conducted an observational study prior to the playback study to encode the pigeon's behavioural repertoire in a variety of contexts. We did not restrict the definition of behavioural variables to

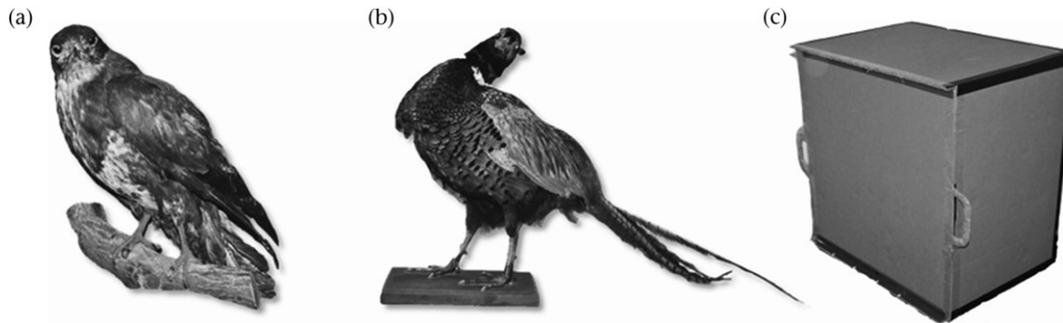


Figure 1. Visual stimuli. Stuffed models of (a) a common buzzard and (b) a pheasant. (c) Both visual stimuli were presented to the pigeons in a cardboard box.

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

Procedure and Set-up

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

predator presence was perceived. Although habituation and dishabituation stimuli in both groups referred to buzzard presence, pigeons in group 3 were confronted with acoustic cues in the dishabituation phase, which we expected to encode lower levels of urgency (compared to previous information in the visual domain) whereas birds in group 4 were presented with visual models that we expected to represent an increased level of urgency (compared to acoustic playbacks during the habituation phase). Every pair of pigeons was tested only once. The experiment for each pair included the baseline, the habituation and the dishabituation phases. At the beginning of each experiment all pigeons except the focal pair were removed from the test aviary and remained in visual and acoustic isolation throughout the experimental phase. Visual and acoustic stimuli were displayed at approximately the same distance (± 0.5 m) to the focal aviary.

Baseline

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

Habituation

As we could not prevent adjacently housed pigeons from eavesdropping on displayed acoustic stimuli, we started with birds that were assigned to groups in which the habituation stimulus was a visual model. Hence, we avoided repeated exposure to acoustic stimuli for birds before they were actually tested. To avoid continuous exposure to visual models for birds except the focal pair, we positioned the cardboard box in such a way that only the focal pair

Table 1

Experimental conditions ('Information' refers to the informational content of the dishabituation stimulus as compared to the habituation stimulus)

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

had full visual access to the model presented inside. Between groups, we included a break of 2 weeks between acoustic habituations and a break of 1 week between visual habituations to avoid the simulation of predator presence at a frequency likely to exceed naturally occurring predator encounters.

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

Dishabituation

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

Statistical Analysis

To examine whether the referent of the stimulus or the sensory mode of presentation has had an effect on the number of trials the birds needed to habituate a Kruskal–Wallis test was applied over all six groups. As the data did not meet the assumptions of normality (Kolmogorov–Smirnov test: $P = 0.687$) or homogeneity of variance (Levene's test: $P = 0.013$), we used two-tailed non-parametric Mann–Whitney U tests, including a Bonferroni correction ($\alpha < 0.0125$) to compare the number of trials to habituation.

To examine whether the birds perceived habituation and dishabituation stimuli as providing different or equivalent information, we compared behavioural responses in both experimental phases. However, as the detailed nature of pigeons' antipredator response has not been described, we first reduced all 17 encoded behavioural variables to independent components using a principal component analysis (PCA). Components with eigenvalues of at least 1 were extracted and a varimax-rotated correlation method was

used. As some of the variables had high loadings on more than one component (>0.4), we had to eliminate eight of our originally measured variables, resulting in nine variables with simple structure (see Table A2 in the Appendix). To ensure consistency in video coding, 10 randomly chosen sample recordings were double coded by a second person who had no knowledge about the stimuli displayed in the videos (visual stimuli were not visible in recordings and videos were presented without sound). The interobserver reliability tests revealed high Cohen's kappa (κ) coefficients for all nine variables (all $\kappa \geq 0.88$, see Table A3 in the Appendix for details). The comparisons of the number of trials to habituation and the PCA were conducted using SPSS v. 17.0.1 (SPSS Inc., Chicago, IL, U.S.A.).

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

RESULTS

Trials to Habituation

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

Behavioural Response

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

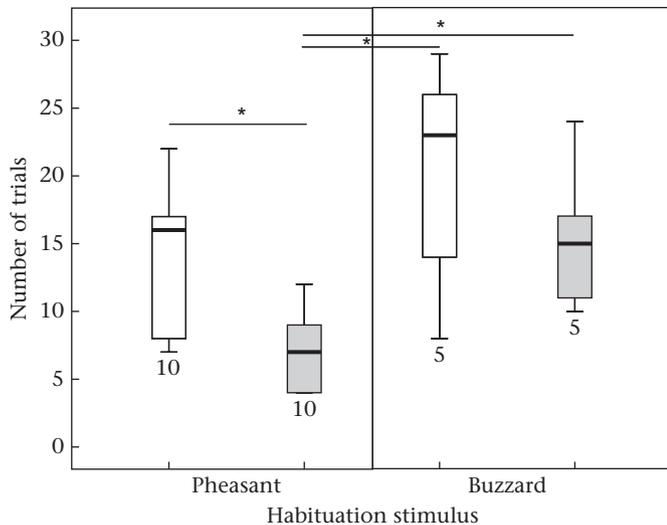


Figure 2. Number of trials the pigeons needed to habituate to pheasant and buzzard stimuli. Box plots in grey indicate acoustic playbacks; box plots in white refer to visual models. Numbers represent the number of dyads that were habituated with each stimulus. *Statistical significance after Bonferroni corrections ($P < 0.013$). Boxes indicate the first and third quartiles. The horizontal line within each box represents the median. Whiskers include values that amount to 1.5 times the height of the box (interquartile range).

(‘nystagmus’), a behaviour that was formerly reported as part of antipredator responses in chicken (Evans 2002). This predator-specific behaviour was performed together with scanning behaviour and was directed to the stimulus or up into the sky.

Effect of Stimulus Order and Sensory Mode

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

pigeons’ past and current experience. We did not find any differences in ‘resting’ (component 1) or ‘partner-directed behaviour’ (component 2) between experimental phases in any of the groups.

DISCUSSION

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

Raptors are frequently present in the pigeon’s environment and produce calls without actually attacking. The birds thus benefit from a reliable perception of the raptors’ presence but they should not always react as they do during predation events (Warkentin et al. 2001). However, if pigeons visually perceive the potential threat in their vicinity (as simulated during visual presentations), the risk of predator attacks, and thus the level of urgency, is increased. The importance of visual information for the inference of urgency and predation avoidance is further supported by the fact that the stuffed models of the pheasant and the buzzard required a similar number of trials for the birds to habituate to them. As the pheasant model was similar in size and plumage colour to the buzzard model, the pigeons might have perceived pheasant models as unfamiliar, disturbingly close and considerably big birds, although they were not interpreted as being as threatening as the buzzard model. The pigeons did not show any

Table 2
Independent variables revealed from principal component analysis

	PC 1	PC 2	PC 3	PC 4
General context	‘Resting behaviour’	‘Partner-directed behaviour’	‘Vigilance’	‘Predatory response’
Percentage of total variance explained	28.8	23.1	14	11
Variables	Retracting neck, fluffing up, sleeping	Approaching partner, feeding	Looking to stimulus, stretching neck and scanning	Looking to stimulus+nystagmus, looking above+nystagmus

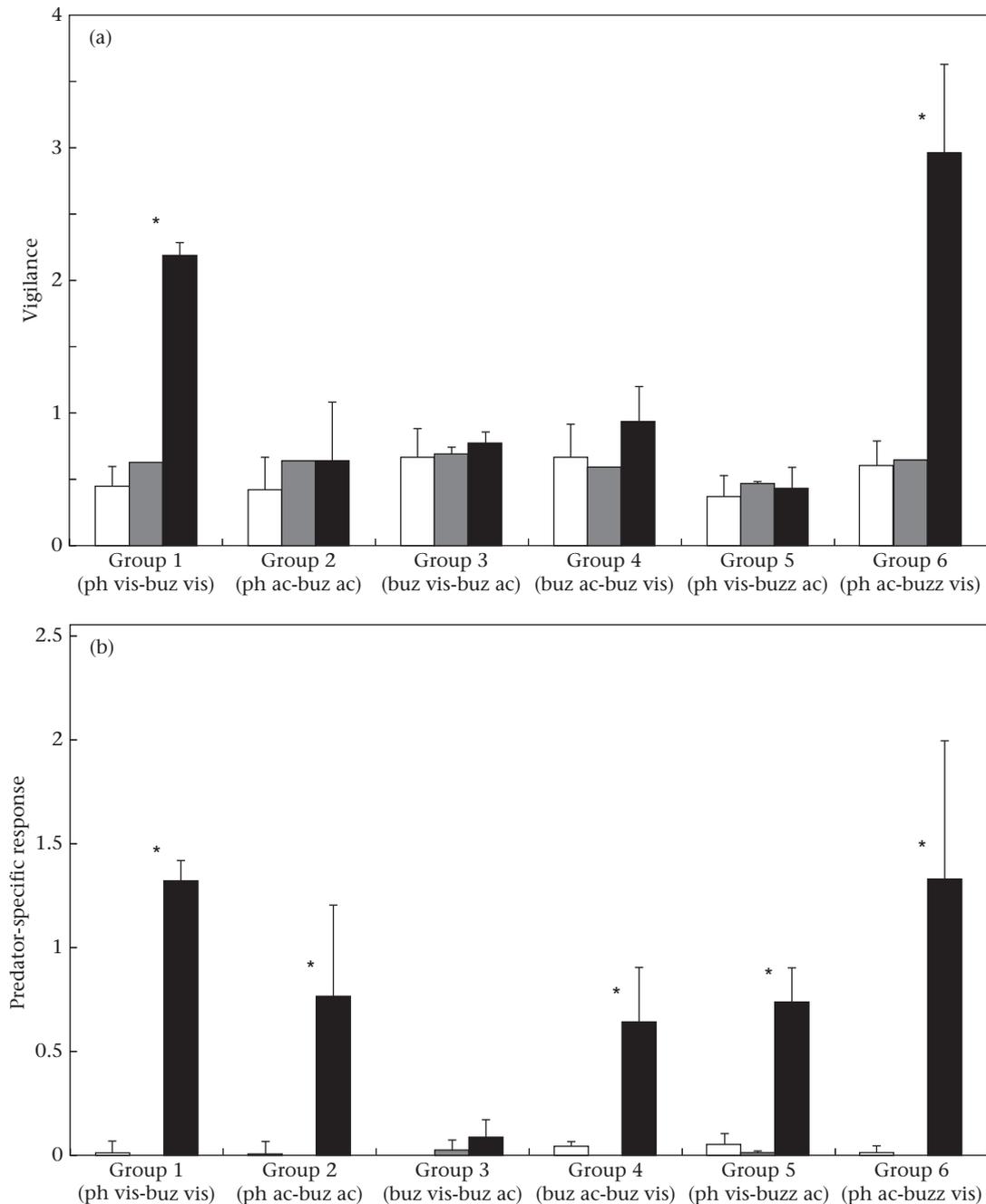


Figure 3. Estimated (a) vigilant and (b) predator-specific responses at the end of the baseline phase (white bars), at the end of the habituation phase (grey bars) and during the dishabitation phase (black bars). Abbreviations below group numbers indicate the stimuli presented during the habituation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

general attention (indicated by scanning and general vigilance) to visual stimuli after acoustic habituation to the buzzard, as if they had already inferred the presence of the buzzard by its calls, but instantly looked at the stimulus (when the box was open) and above (after the box was closed) and performed characteristic scanning behaviour. This predator-specific scanning behaviour manifests in rapid back and forth head movements that facilitate fast depth perception by motion parallax. Especially for birds of prey with laterally placed eyes and little binocular overlap, motion parallax is thought to function to estimate predator distance reliably (Evans 2002). As the position of stimulus presentation was kept constant in both sensory modes, we consider it unlikely that any variables (e.g. distance to playback source/models)

other than the sensory mode encoded different levels of urgency in our study. However, a possible alternative interpretation of the present results may be considered. As pigeons reacted with predator-specific scanning behaviour also to visual presentations of the buzzard that followed buzzards' calls, it may be argued that birds did not integrate predator cues cross-modally but only showed reliable discrimination of predator (buzzard) and nonpredator (pheasant) within one sensory mode and that they generally perceive visual displays as being more urgent. However, we consider this explanation highly unlikely for two reasons. First, the pigeons' behavioural responses were composed of two independent components (vigilance and predator-specific scanning). If we take both independent

variables into account, the birds did not show the same responses whenever visual buzzards were presented. Although they responded with predator-specific scanning behaviour to buzzard models after they were habituated to buzzard calls (probably to gain more information about the exact distance of the threat), we did not find increased levels of general vigilance. In contrast, when visual buzzard presentations followed pheasant stimuli, pigeons were significantly more vigilant, engaged in scanning the surroundings and additionally performed predator-specific scanning during dishabituation. Second, the pigeons needed comparable numbers of trials to habituate to buzzard calls and to the buzzard model, suggesting that these stimuli were perceived as being equally disturbing when presented alone and for the first time. What we cannot (and do not) claim is to have identified the level of discrimination. Our results show that pigeons recognized predatory stimuli. The exact referent of the applied functional class, namely whether pigeons actually recalled mental representations of buzzards in particular, aerial predators or a predator in general has to be addressed in further studies.

Taken together, the present study suggests that advanced mechanisms of contextual interpretation of external information in the context of predation can also be found in species that do not use specific signals such as alarm calls. This extends the cognitive abilities found in nonalarm-calling species and supports the previously found disparity in cognitive abilities of signallers and receivers in highly vocal species.

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

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Table A1

Response variables

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

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

Table A2

Rotated component matrix

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

Loadings of original variables on the different components are presented. Loadings higher than 0.4 are highlighted in bold.

Appendix

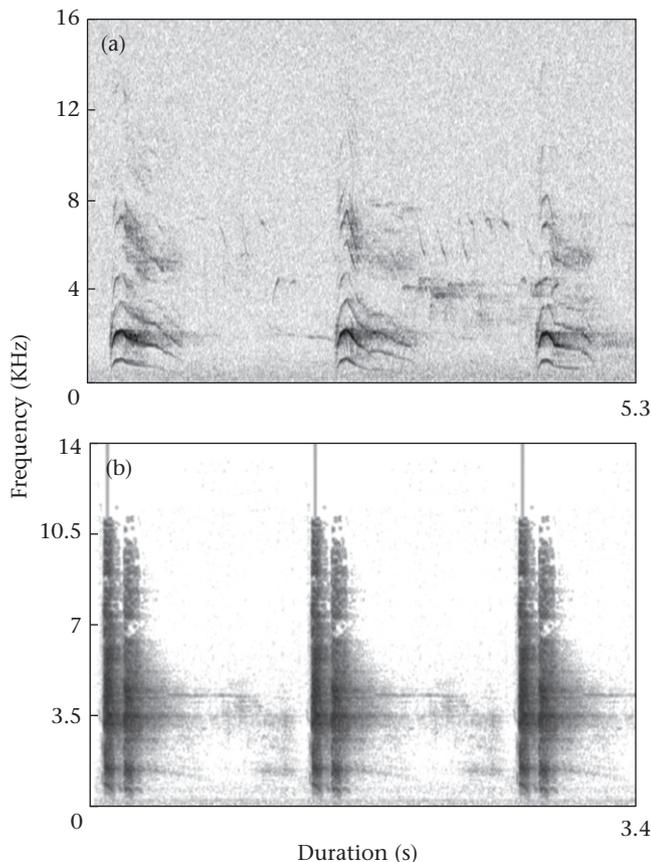


Figure A1. Spectrograms of acoustic stimuli: (a) buzzard territory calls, (b) pheasant territory calls.

Table A3

Interobserver reliability

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

Cohen's kappa coefficients are given for single variables.