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Using video playback to investigate the social preferences of rooks, *Corvus frugilegus*

CHRISTOPHER D. BIRD* & NATHAN J. EMERY*†

*Sub-department of Animal Behaviour, Department of Zoology, University of Cambridge †School of Biological & Chemical Sciences, Queen Mary, University of London

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It is important for social animals to be able to discriminate between group members. Much is known about vocal social communication through auditory playback techniques; however, visual information may also be important for conspecific recognition in the absence of auditory cues. Within the visual channel both static and dynamic features may play important roles in individual recognition. Rooks are a social corvid and they live in large colonies and form long-term pair bonds, both requiring the ability to recognize individuals. In this study we investigated whether rooks 'see' a digital image as a representation of a real animal, using visual playback techniques and a new paradigm for assessing social preferences that uses stimuli differing in features such as whether they are live animals, static or video images, or stuffed models. We presented the rooks with two different stimuli of the same category and recorded the amount of time they observed each stimulus. Rooks preferred to look at a live bird, static or video image of a bird, and a stuffed model over an empty compartment. Rooks also showed a clear preference for a strongly affiliated conspecific (e.g. their partner) over a nonaffiliated conspecific. This preference was not apparent when we presented subjects with static images; however, the preference was seen with video, indicating that rooks can recognize individuals in video. We conclude that video playback is a useful technique for investigating rook social behaviour.

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Ethologists have used video playback as a tool since the 1960s; however, recent advances in digital image technology and better understanding of the visual systems of animals have made video playbacks a more useful technique of late. Technical advances are occurring in all visual domains: photographs, video and computer-generated software, where the user can manipulate the stimulus and define precisely its parameters. Digital photographs and video have also benefited from improvements in image resolution, such as high-definition video. Advances are also occurring in the playback of visual media; computer monitors are now used instead of slide projectors. Cathode-ray tube monitors were used originally but were

Correspondence: N. J. Emery, School of Biological & Chemical Sciences, Queen Mary, University of London, London E1 4NS, U.K. (email: n.j. emery@qmul.ac.uk). C. Bird is at the Sub-department of Animal Behaviour, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, U.K.

problematic for species with high flicker fusion frequencies (humans ~ 60 Hz, birds > 100 Hz), as they typically refresh at 60 Hz, causing a bird to view the image as a series of snapshots rather than as naturally moving footage. In addition, flicker may negatively affect a bird's welfare (Smith et al. 2005). The majority of video playback studies now use LCD TFT monitors, which circumvent the problem of flicker as they do not refresh in the conventional manner.

The problem of flicker has been removed by using LCD monitors; however, other factors such as colour, brightness and lumination must also be considered. Although birds have a tetrachromatic visual system, the spectral sensitivity of their fourth visual pigment may have a bias that varies from violet (e.g. Corvidae, Tyrannidae) to ultraviolet (e.g. Passeridae, Psittacidae) in different species (Odeen & Hastad 2003). Those species whose short wavelength sensitivity is biased towards violet may have fewer problems recognizing images displayed on LCD monitors, which output colours tuned to the human trichromatic visual system.

Brightness or luminance must also be controlled as these parameters may affect image preference (Humphrey 1972). Finally, viewing distance must be considered. Hens were unable to recognize a familiar flockmate unless they were closer than 30 cm and could 'inspect' each other using the frontal view (Dawkins 1995, 1996). However, at very close distances, birds have more opportunity to view the flat video image obliquely, thereby distorting its shape. Both stereoscopic and motion parallax cues used in depth perception by birds will reveal the flatness of the video screen (De Valois & De Valois 1988).

Most experiments with static visual stimuli have focused on learnt discriminations, in which an animal is trained to discriminate between two images or sets of images and their generalization to novel images (Herrnstein et al. 1976; Dasser 1987). Although there is little doubt that birds can discriminate individuals during their natural interactions, studies of chickens found no evidence that they learnt to discriminate slides of familiar conspecifics more quickly than slides of unfamiliar conspecifics, thereby concluding that the chickens did not see the slides as representations of group members (Bradshaw & Dawkins 1993; Dawkins 1996). Similar conclusions were drawn from a study by Ryan & Lea (1994) on pigeons and chickens.

A number of studies on pigeons and chickens also failed to elicit spontaneous natural responses through static image presentation (Ryan & Lea 1994); however, moving images are often more successful at eliciting spontaneous natural responses, particularly in those species for whom motion is the major component of their visual recognition system. For those species previously tested, video has not necessarily facilitated individual recognition of conspecifics where static images have failed. Domestic hens did not spontaneously discriminate familiar and unfamiliar conspecifics shown on video (D'Eath & Dawkins 1996) and could transfer discrimination from various hens and objects to video only when the two stimuli to discriminate had different colours (Patterson-Kane et al. 1997). There are, however, lessons to be learnt from negative results (Schlupp 2000), and often these studies highlight important design considerations (D'Eath 1998; Fleishman et al. 1998; Fleishman & Endler 2000; McGregor 2000; Oliveira et al. 2000a, b). These considerations are important when assessing the applicability of using video playback for a new species, particularly an avian

Rooks are highly gregarious birds, roosting and foraging in large flocks of up to 60 000 individuals. Within these flocks, individuals form a close bond with another individual (Emery et al. 2007). Individual recognition is an important component of everyday life, yet the relative contribution of visual and vocal cues for this recognition is unknown. This study aimed to determine whether rooks show the same social preference towards still pictures, video or stuffed models as they do towards live conspecifics. If the rooks find these stimuli equivalent to the live condition we predicted that they should show the same spontaneous image preferences when given choices in the live condition as when given choices with static pictures, videos or stuffed models.

Preference studies usually involve some training using a food reward to maintain the response during testing (e.g. Humphrey 1972); however, no pretraining was required in this study. Visually isolated rooks naturally look through small openings to see the rest of the group (Bird, personal observations), dispensing of the need for pretraining, whereas the stimuli themselves should act as social rewards to a visually isolated bird, so maintaining the preference choice (Anderson 1998; Galoch & Bischof 2006).

A good indication of visual preference may be looking time or frequency; however, it is very difficult to determine where a bird is looking or when it is attending to an image, because of the positions of their eyes and their wide visual field (Dawkins 2002). The head movements associated with peering are distinguishable from other head movements so that the amount of time looking through a hole at a particular image may be accurately measured. Other studies have used peering through a hole as a measure of image preference (Cooper & Hosey 2003) or as a measure of attention span (Range & Huber 2007; Scheid et al. 2007).

METHODS

Subjects

Eleven rooks (nine female and two male) were used as subjects; however, only nine of these birds were used for each condition due to husbandry reasons during the experiment. All birds were 3 years of age at the time of testing and had no previous experience with image presentation or preference choice experiments. They formed part of a group of 15 hand-raised rooks kept in large outdoor aviaries ($20 \times 8 \times 3$ m) at the Sub-department of Animal Behaviour, Madingley, U.K. These aviaries were furnished with numerous high and low perches, multiple areas of shelter including roof cover and nesting boxes and a variety of floor substrates including grass and gravel. Food and water were provided ad libitum outside of test trials, consisting of a diet of pasta, egg, cheese, assorted vegetables and bread. The aviaries also contained a variety of easily manipulated toys for added environmental enrichment.

Apparatus

The subjects were tested in a naturally lit, single chamber ($3 \times 1.6 \times 1.5$ m) in which they were visually and physically isolated from the rest of the group (see Fig. 1); however, a small bowl of seeds was provided along with water during trials.

A box was mounted on the front wall of the chamber in which two holes (2 cm diameter) were cut. At the back of the box, at a distance of 50 cm from the holes, the subjects could see either a 24-in. TFT monitor (Samsung LCD SM244 T, Samsung Electronics, South Korea) for the static and video conditions (Fig. 1a) or an adjacent chamber $(2\times2\times3~\mathrm{m})$ containing the live or stuffed stimuli (Fig. 1b). We presented the choice stimuli simultaneously in each condition, and the monitor or chamber was divided in half such that the stimuli were separated by an opaque

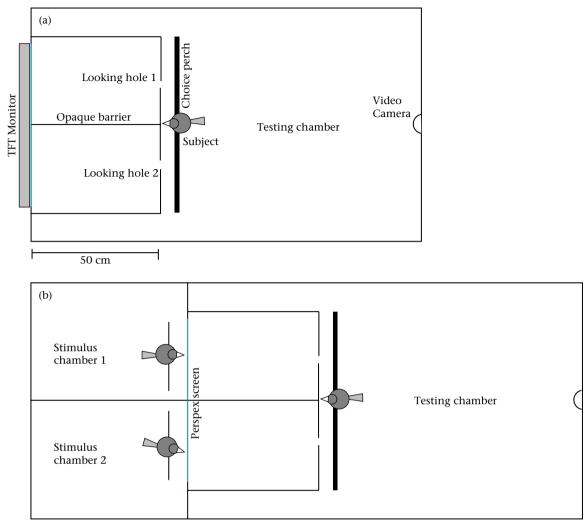


Figure 1. Schematic of the experimental set-up. (a) Static/video condition. (b) Live/stuffed condition. Drawings not to scale.

wooden barrier allowing the subjects to see only one stimulus from each viewing hole.

A perch (1.65 m high) stood directly in front of the box such that when a bird landed on the perch, the holes were at its natural eye level. The behaviour of the subject was monitored remotely via a camera (Atom Dome, Model AHC, CSP Technology Ltd, Scunthorpe, U.K.) positioned at the back of the testing chamber and recorded onto digital videotape for later analysis.

We presented static images on the monitor using Microsoft Office PowerPoint, controlled by a PC laptop (Pegasus M3C M3603, Rock Direct, Warwick, U.K.). We presented video images on the monitor from highdefinition videotape played through an HD camcorder (Sony HDR-HC1E, Sony Corp., Tokyo, Japan).

Stimuli

The unfamiliar birds used as stimuli for this study were one male and one female hand-raised rook. These birds were 4 years of age at the time of the study and are part of a group of nine hand-raised rooks housed in a second large outdoor aviary, which was visually but not audibly separated from the subject birds.

Live birds

For experiment 1, the stimulus bird was an unfamiliar rook chosen to match the sex of the subject. We chose an unfamiliar stimulus rook to control for any preformed affiliative or aggressive relationships between the subject and the stimulus, while the sex was matched to remove any effect of sexual preferences.

For experiment 2, the stimulus birds were the subject's partner or closest affiliative member of the group (of the nine subjects, two had a same-sex affiliative partner (female-female pairs) and seven had a different-sex partner (male-female pairs)) and one of the rooks used as a stimulus in experiment 1 (chosen to match the sex of the partner). The sample size was too small to make comparisons between the strength of the preference between same sex-different sex pairs, and we collected data outside of the breeding season so that we did not expect any confounding effects of reproductive status on subject motivation.

Static images

Photographs of the stimulus birds were taken with a digital camera (Canon SLR EOS 300D, Canon, Inc., Tokyo, Japan) at 4-MP resolution. The photos showed the birds in a perched position and were matched as closely as possible for posture. Images of the empty compartment were taken at the same resolution. Composite bird—background images were created using Adobe Photoshop CS2 such that different birds were positioned on the same background to control for background preferences. The image contrast levels were set at the Photoshop automatic preset and the monitor brightness levels were kept constant throughout. The images were saved and presented in uncompressed JPEG format. The stimuli were presented as life size.

Video

We recorded videos of the stimulus birds in highdefinition 1050i format (1440 × 1080 resolution). All recordings had the same background, part of the aviary containing a perch, similar but not identical to the background used for the static images. We recorded individual birds continuously for 1 h each, and subsequently clipped a 30-min video from each recording, taking out sections of the video when the bird moved off the perch and disappeared out of view and sections in which the bird performed pair-specific behaviour such as the bowing display (Coombs 1978). The resulting 30-min video contained nonrepeating footage in which the bird never disappeared out of view for more than a couple of seconds, did not change its distance from the camcorder, did not show any impossible movements such as suddenly appearing or disappearing and did not perform any specific affiliative displays. We removed sound from the recordings and edited using Sony Vegas video editing software. We rendered two 30-min edited videos side by side with a 1-cm space between them in MPEG2 HD format. Then we re-recorded them back to high-definition videotape and played them on the monitor so that each video occupied half of the monitor screen.

Stuffed model (used only for experiment 1)

We borrowed a taxidermically prepared model of an adult rook mounted on a wooden stand from the University Museum of Zoology, University of Cambridge, and used it as a stimulus.

Procedure

We conducted the experiments between July and November 2006. Before the experiment began, we familiarized the birds with the testing chamber, both with the monitor present and absent and with the monitor switched on and switched off (white screen).

At the start of the experiment, we initiated the image presentation and the bird entered the testing chamber (in the live condition, we allowed the stimulus birds to settle for 30 min before the subject bird entered the choice chamber). We required that the subject bird look through

both holes before the trial began. On occasions when the bird failed to look into both holes within 15 min of entering the chamber, we terminated the trial and repeated it the following day, although this happened rarely. After looking through both holes, we required that the bird return to the centre of the perch before the 30-min trial began. The trial ended after 30 min and we released the birds from the testing chamber. If, during the 30-min trial, a bird spent more than half of the time off the perch, we discarded the data and retested the bird at a later date.

Each bird underwent only one trial per day. For each image pair, all birds underwent two trials, with the positions of the two images (either on the left or on the right) reversed. This balanced design allowed any potential side biases to be eliminated through averaging the results of the two trials when analysing the data. The presentation order of the two trials and the order in which the birds were tested were pseudorandomized. We scored the trials using Observer software (version 5.0, Noldus Information Technology, Wageningen, The Netherlands), recording two test measures indicating preference: number of looks through the holes and total time looking through holes.

Data Analysis

To test whether each subject preferred one stimulus over another, we looked at the rooks' visual behaviour, either number of looks or total time looking at one stimulus divided by the total for both stimuli. We averaged these percentages for the two trials and used the difference from 50% (as would be found if the birds showed no preference between the two stimuli) as a preference score. We tested these data for normality using the Kolmogorov-Smirnov test and analysed them using one-sample t tests (against a null value of 0 preference). We also measured the mean duration of looks and compared these data between the two stimuli using paired t tests. We used one-way ANOVA to compare the effect of condition on the strength of any preference. We made planned comparisons between live and other conditions using Fisher's LSD post hoc tests as we predicted the strongest preference to be for the live stimulus. In addition we performed a twoway ANOVA to test the general hypothesis that conditions have no effect on looking behaviour. As we expected all conditions in experiment 2 to have the same effect on looking behaviour, we did not perform the two-way ANOVA in this case but, rather, subjected our results to a sequential Bonferroni correction using the Hochberg procedure to avoid type 1 errors.

RESULTS AND DISCUSSION

Experiment 1: Do Rooks Prefer to Look at a Novel Conspecific Rather Than an Empty Compartment?

We assessed preference for an unfamiliar conspecific over an empty compartment using four categories of stimuli: live, static picture, video and stuffed bird. In each of these comparisons the conspecific and the compartment were of the same category, for example, a static picture of a conspecific was compared to a static picture of an empty compartment. We predicted that when visually isolated, rooks would prefer to look at a conspecific rather than an empty compartment for all of these categories of stimuli. To address the possibility that rooks simply prefer to look at any interesting stimulus over an empty compartment, we included a control condition in which the choice was between a static image of an empty compartment and a static image of a black oval shape with roughly the equivalent number of black pixels as the static picture of the rook (but lacking any bird-like features).

Results

In the live condition, rooks looked significantly more often at the conspecific over the empty compartment $(7.67 \pm 2.69\%)$ preference; one-sample t test: $t_8 = 2.86$, P = 0.021) and for a longer total duration $(7.49 \pm 2.93\%)$ preference; one-sample t test: $t_8 = 2.56$, t = 0.034). There was no significant difference in the mean look duration between the two stimuli (paired t test: $t_7 = 0.35$, t = 0.73, Fig. 2), indicating that the longer total look duration was due to the greater number of looks towards the conspecific, not the length of the inspections.

The results of the static picture condition, were similar to those of the live condition. Rooks showed a preference to look towards the static picture of a conspecific, looking more often at the static image (one-sample t test: $t_8 = 2.55$, P = 0.034, Fig. 3) and for a significantly greater total duration (one-sample t test: $t_8 = 2.92$, P = 0.019; Fig. 4) than at the image of an empty compartment. There was no significant difference in the mean look duration between the two stimuli (paired t test: $t_8 = 0.08$, P = 0.94, Fig. 2).

In the video condition, rooks showed a looking preference towards the conspecific over an empty compartment; however, the difference was significant only for total time looking (one-sample t test: $t_8 = 3.96$, P = 0.004; Fig. 4), not for the number of looks (one-sample t test: $t_8 = 1.45$, P = 0.186). In addition, the mean look duration was significantly longer towards the video of the conspecific compared to the video of the empty compartment (paired t test: $t_7 = 1.45$, P = 0.0002, Fig. 2). In the stuffed condition, rooks looked for a longer total duration (one-sample t test: $t_8 = 2.31$, P = 0.05) at the conspecific over the empty

compartment, with a nonsignificant trend for the number of looks (one-sample t test: $t_8 = 2.10$, P = 0.07). There was no significant differences in the mean look duration towards the stuffed model and the empty compartment (paired t test: video: $t_8 = 0.81$, P = 0.44, Fig. 2).

In the control condition, there was no preference for the black oval shape over the empty compartment for number of looks (one-sample t test: $t_8 = 0.67$, P = 0.522) or the total time spent looking (one-sample t test: $t_8 = 0.29$, P = 0.78) and no difference in mean look duration (paired t test: $t_5 = 1.75$, P = 0.14, Fig. 2).

A two-way ANOVA allowed us to reject the general hypothesis that condition had no effect on looking behaviour (number of looks ANOVA: $F_{4,30} = 2.46$, P = 0.067; total time looking ANOVA: $F_{4.30} = 2.79$, P = 0.044). For all conditions that showed a looking preference for the conspecific over the empty compartment (all except control), we tested the effect of condition on the strength of the preference, revealing that there was no difference between the live condition and the static, video or stuffed condition for either number of looks (ANOVA: $F_{3.32} = 0.617$, P = 0.61) or total time looking (ANOVA: $F_{3.32} = 0.57$, P = 0.64). Comparing the mean look duration towards the conspecific, there was a significant effect of condition (ANOVA: $F_{4,25} = 4.52$, P = 0.007), with looks significantly longer in the live condition than in the static (Fisher's LSD: P = 0.0001), stuffed (Fisher's LSD: P = 0.029) or control condition (Fisher's LSD: P = 0.01) but not the video condition (Fisher's LSD: P = 0.114).

Discussion

Rooks preferred to look more often and for longer at a live unfamiliar conspecific than an empty compartment. The preference for the conspecific was also elicited by static pictures, video and a stuffed model. There was no significant difference in mean look duration for the bird over the empty compartment in any of the conditions except for video. This meant that although the total time looking towards the bird was significantly longer than towards the empty compartment for all conditions, this stemmed from a greater frequency of looking rather than longer individual looks in most cases. Rooks forage in large flocks, gaining social benefits such as increased predator vigilance. To use visual information from others in the flock, one must be in

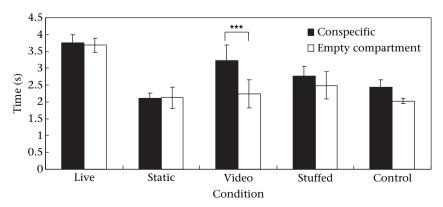


Figure 2. Mean (\pm SE) look duration for all conditions (live, static, video, stuffed and control) in experiment 1. ***P < 0.001. Black bars: conspecific; white bars: empty compartment.

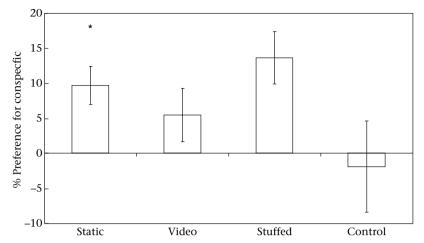


Figure 3. Mean (\pm SE) preference score for the number of looks through the hole across all conditions (static, video, stuffed and control) in experiment 1. *P < 0.05.

visual contact with them. Constant checks may be required to update this information; however, a short check may be sufficient, and so the actions of a novel bird may not hold one's attention for very long.

Subjects showed no preference for the black oval over the empty compartment for any test measure. This control condition therefore reduces the possibility that the rooks prefer to look at any novel object. The black oval was approximately the same size as the rook stimuli and contained a similar number of dark pixels compared to the various digital bird stimuli. This result suggests that specific features are necessary to elicit an appropriate looking preference. The preference for the bird over the empty compartment does not necessarily mean that subjects categorized the various stimuli as representing another rook. Indeed in this basic design, it is possible that any interesting object containing various features would also have elicited looking preferences compared to an empty compartment.

The live condition was different from the other conditions because the stimulus birds were audible to the subject, whereas the sound was removed or not present

in the other conditions. The lack of sound in the static picture, video or stuffed conditions did not seem to have a significant effect on the strength of the preference compared to the live condition.

Other studies have shown that a subject's spontaneous behaviour, such as courtship displays in pigeons, are more vigorous when presented with video images than with still frames (Shimizu 1998). Unlike the static condition, when rooks were presented with video there was no difference in the number of looks towards the bird compared to the empty compartment. However, the mean duration of the looks and the total duration of looks were longer towards the bird, indicating that the video of the conspecific kept the subjects' attention longer.

Experiment 2: Do Rooks Prefer to Look at Their Partner over a Nonaffiliated Conspecific?

Rooks are a life-long pair-bonded species; therefore we predicted that they would prefer to look at their partner over a nonaffiliated conspecific.

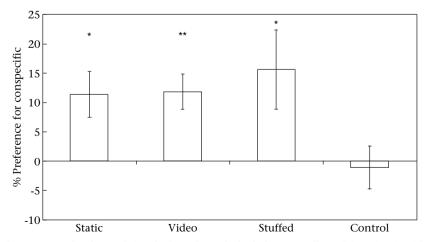


Figure 4. Mean (\pm SE) preference score for the total time looking through the hole across all conditions (static, video, stuffed and control) in experiment 1. *P < 0.05, **P < 0.01.

Results

In the live condition, rooks preferred their partner over an unfamiliar conspecific for number of looks $(16.97 \pm 4.20\%)$ preference; one-sample t test: $t_8 = 4.04$, P = 0.004) and total time spent looking (16.97 \pm 4.15% preference; one-sample t test: $t_8 = 4.02$, P = 0.004), even when corrected for multiple tests. However, there was no difference in mean look duration between the two stimuli (paired t test: $t_7 = 0.49$, P = 0.64, Fig. 5).

In the static picture condition, the rooks did not show a preference for their partner for the number of looks $(8.43 \pm 6.09\%)$ preference; one-sample t test: $t_8 = 1.39$, P = 0.20) or total time spent looking (7.28 \pm 6.57% preference; one-sample t test: $t_8 = 1.11$, P = 0.30). However, in the video condition, rooks looked longer at their partner rather than at an unfamiliar conspecific (8.60 \pm 3.19% preference; one-sample t test: $t_8 = 2.69$, P = 0.027), although this fell just short of significance when the sequential Bonferroni correction was applied. They also showed a significantly higher mean look duration towards their partner (paired t test: $t_7 = 3.12$, P = 0.017, Fig. 5). There was no difference in the number of looks towards the two stimuli for the video condition $(4.38 \pm 3.50\%)$ preference; one-sample t test: $t_8 = 1.25$, P = 0.25). Comparing the strength of the preference between the live and the video conditions, there was no significant difference between the two conditions for number of looks (paired t test: $t_6 = 1.82$, P = 0.12) or total time looking (paired t test: $t_6 = 1.06$, P = 0.33). Comparing the mean look duration towards the partner stimulus, there was a significant effect of condition (ANOVA: $F_{2,22} = 5.24$, P = 0.014), with looks significantly longer in the live condition than in the static condition (Fisher's LSD: P = 0.004), but no difference between the live and the video conditions (Fisher's LSD: P = 0.102). Comparing the mean look duration towards the unfamiliar conspecific there was a significant effect of condition (ANOVA: $F_{2,21} = 14.69$, P = 0.0001), with looks significantly longer in the live condition than in the static picture (Fisher's LSD: P = 0.0001) or video condition (Fisher's LSD: P = 0.0001).

Discussion

The number of looks and duration of looking indicated a preference for the partner over the unfamiliar bird in the live condition. Rooks may prefer to look at their partners to maintain close proximity to them and may use visual information to coordinate behaviour within the pair (Emery et al. 2007). None of the test measures showed a preference for the partner over the nonaffiliated rook in the static condition. This suggests that individual recognition is not possible with static pictures for rooks. Rooks may use both featural and motion information to recognize individuals; however, motion is lacking in static images. The subjects may therefore have recognized the image as a rook, but possessed no information about its identity. This is perhaps surprising given that Jacky dragons appear to distinguish between familiar and unfamiliar conspecifics using static morphological features alone (Van Dyk & Evans 2007).

When presented with the preference choice in the video condition, subjects looked longer (total duration and mean look duration) at their partner than at the nonaffiliated bird; we found no difference in the number of looks. This suggests that individual recognition is possible for rooks when presented with video, but even if it is not, some visual features of the partner holds the subject's attention longer. As the nonaffiliated conspecific was from a different group to the subject and its partner, it is possible that the discrimination made did not represent individual recognition but rather discrimination based on group membership. If this were the case, this would suggest some subtle movement or behaviour common to all birds within a social group. This seems unlikely. It is not clear why there was no difference in the number of looks between the partner and the nonaffiliated bird in the video condition when this difference was present in the live condition; however, if sufficient information is gained from a prolonged look, then fewer shorter looks would not be required.

The evidence that rooks can spontaneously recognize individuals through video supports the findings of other studies with similar conclusions: female Japanese quail

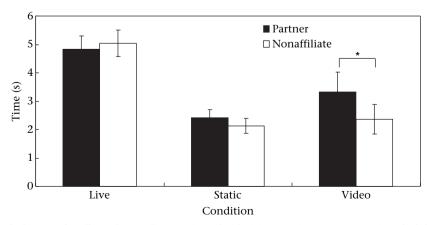


Figure 5. Mean (\pm SE) look duration for all conditions (live, static and video) in experiment 2. *P < 0.05. Black bars: partner; white bars: nonaffiliated conspecific.

affiliate with the same live male that they have seen mate on video (Ophir & Galef 2003). Male zebra finches prefer video of an unknown female over their mate, whereas female zebra finches prefer video of their mate over an unknown male (Galoch & Bischof 2006; Swaddle et al. 2006), although the female choice of video was the opposite to that seen in the live condition (Swaddle et al. 2006).

General Discussion

Although the findings that rooks prefer to look at a conspecific over an empty compartment and at their partner over a nonaffiliated conspecific are interesting in their own right, the main aim of the study was to investigate the ability of digital stimuli, either static images or video, to represent conspecifics or individuals. We have shown that static images of a conspecific elicit a looking preference over background, but that spontaneous recognition of individuals was not possible with static pictures. This is consistent with previous findings on a number of bird species, including pigeons and domestic hens (see Bovet & Vauclair 2000 for a review). However, we have also shown that video (without sound) is sufficient to elicit spontaneous individual recognition in rooks. Vocal cues in the absence of visual cues can be used for individual discrimination in spectacled parrots (Wanker et al. 1998), and juvenile rooks can recognize sibling vocalizations (Roskaft & Espmark 1984). Audio and visual cues may be used separately to identify individuals, especially in noisy environments (auditory or visual noise), but it is likely that in the wild they are used in combination when both are available (see Partan & Marler 2005 for a review). Adding acoustic information to video playback often enhances an animal's reaction to the clips (Galoch & Bischof 2007), indicating a combinative effect of the two channels in communication. Additional information may be revealed from an animal's response to a mismatch of the two channels (Watanabe & Jian 1993).

In rook displays, the two channels seem to be strongly coupled such that a 'caw' is usually accompanied by a bow display (Coombs 1978). The significantly longer mean duration of looks in the video condition for both experiments may be caused by the visual appearance and the call being decoupled (as audio was removed), violating the birds' normal expectation. Such decoupling does not occur in any of the other conditions. The ability of rooks to recognize individuals in video but not static images suggests the importance of dynamic features in discrimination. Motion may be more salient than static features and studies have shown that bird vision is highly tuned to movement (Dittrich & Lea 1993). Indeed, pigeons can categorize different types of movement using point light cues and can transfer between point light and full detail displays (Lea & Dittrich 1999). Movement may aid discrimination by triggering some attentional process that makes integration across features easier (Dittrich et al. 1998).

The inability of rooks to recognize individuals in static pictures spontaneously is not completely surprising as even humans with no experience of photographs fail to recognize individuals (Miller 1973; Deregowski 1989). The rooks were also naïve with respect to image playback.

Recognition of static images may improve with experience of presentation with video or multiple static views. For example, pigeons trained to discriminate video scenes of two conspecifics transferred the discrimination to still scenes (Jitsumori et al. 1999). This suggests that although motion may be the dominant cue used to discriminate video images, information that is invariant across static and dynamic conditions can be used following experience. Conspecifics may be recognized in static images; however, discrimination of individuals in static images has been shown only after experience or training (see Van Dyk & Evans 2007), leading to the possibility that 'correct' responses may in such cases be based on irrelevant stimulus features rather than recognizing the image as a representation of the real individual. Social preferences probably occur through processing and integrating a collection of stimulus features. Our study supports this conclusion and also provides evidence that birds are capable of spontaneous individual recognition through video when presented in the absence of flicker, at an appropriate viewing distance and at a high resolution. The 'peephole' technique established here seems to be a useful tool in investigating birds' looking behaviour and preferences. These findings and techniques will pave the way for the use of visual playback to be implemented in other aspects of corvid cognition and behaviour research.

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