Successive negative contrast in a bird: starlings' behaviour after unpredictable negative changes in food quality

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In a successive negative contrast (SNC) procedure, subjects used to a familiar contingency are unexpectedly shifted to a less favourable one. Typically, mammals in the new condition show lower anticipatory and consummatory responses than controls that only experience the low contingency, but similar experiments in birds have failed to show SNC. We investigated SNC in European starlings, *Sturnus vulgaris*. In experiment 1, birds that were shifted from mealworms (preferred food) to turkey crumbs (less preferred food) consumed less of the turkey crumbs, and showed elevated activity and exploratory feeder probing with respect to unshifted starlings exposed throughout to turkey crumbs. This is the first report of consummatory SNC in birds. In experiment 2, two groups differed in the amount of information. Initially, both groups encountered simultaneously one hopper with mealworms and three with turkey crumbs. The mealworm hopper was colour coded in group 'cued' but not in group 'uncued'. After a shift, all four feeders contained turkey crumbs and were signalled by the colour associated with turkey crumbs before the shift. The two groups did not differ in postshift consumption, and increased overall activity similarly after the shift. Exploratory feeder probing, however, increased significantly less in group cued than in group uncued, consistent with the view that informed animals adjusted faster (ceased searching for the preferred food) to the new conditions. The dissociation between exploration and consumption in their sensitivity to available information during the reward downshift is discussed in terms of the adaptive implications of SNC.

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It is now well established that animals' preferences between food-signalling stimuli are sensitive to incentives present in the background context but absent at the time of choice (e.g. Waite 2001; Pompilio 2004; Freidin 2007). This sensitivity to background alternatives has sometimes been regarded as paradoxical from rationality or optimality standpoints, because it can cause behaviour to be inconsistent across contexts, and can lead to preference for suboptimal options (e.g. Shafir 1994; Waite 2001; Bateson et al. 2002, 2003; Marsh & Kacelnik 2002; Shafir et al. 2002; Pompilio 2004; Freidin 2007).

The notion of relative valuation of incentives has been an active topic of research in animal experimental psychology since the early 20th century (e.g. Tinklepaugh 1928). Psychologists have mainly focused on proximal questions about incentive relativity, such as the factors that modulate it and the mechanisms that allow relative responding to reinforcement events (see Flaherty 1996 for an

extensive review); however, much less attention has been directed towards its functional implications.

One iconic phenomenon in the incentive relativity literature is the so-called successive negative contrast (SNC) effect. During an SNC procedure, one group of subjects is unexpectedly shifted from a higher to a lower quality and/or quantity of reward (by 'unexpected' or 'surprising' shifts, we mean that the higher reward is omitted while there are situational and/or discrete stimuli indicating its impending presentation); the SNC effect is characterized by those animals reducing their anticipatory and/or consummatory responses towards the postshift lower-value reinforcement significantly below the performance level of controls that received only the lower incentive from the start (Flaherty 1996, pp. 19–53). This pattern of behaviours has been reported in laboratory rats, *Rattus norvegicus* (e.g. Crespi 1942), laboratory mice, *Mus musculus* (e.g. Mustaca et al. 2000), didelphid marsupials of two species, *Lutreolina crassicaudata* and *Didelphis albiventris* (e.g. Papini et al. 1988), domestic dogs, *Canis familiaris* (Bentosela et al., in press), and human babies (e.g. Kobre & Lipsitt 1972), among other mammals (see Papini 2003).

The typical mammalian performance during SNC conflicts with the Thorndakian law of effect (Amsel 1992; Papini 1997) that states

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that a higher reinforcement history in a given situation causes higher performance in the same or similar conditions through the formation of more intense associations between operant behaviour and stimuli (Thorndike 1911). In SNC, subjects used to receiving the higher incentive and shifted to a lower reward perform below controls that had always received the lower incentive. Curiously, pigeons, *Columba livia* (Papini 1997) and other nonmammalian vertebrates, such as toads, *Bufo arenarum* (e.g. Muzio et al. 1992; Papini et al. 1995), turtles, *Geoclemys reevesii* (e.g. Papini & Ishida 1994) and goldfish, *Carassius auratus* (e.g. Lowes & Bitterman 1967; Couvillon & Bitterman 1985), have been shown to respond to SNC situations as expected from the classic law of effect. In these cases, individuals used to receiving the higher reward and downshifted afterwards do not perform below the controls' level. For instance, Papini (1997) tested pigeons in a key-pecking task where birds were shifted from a large to a small reward, but subjects gradually adjusted their behaviour towards the controls' performance, hence failing to follow the SNC pattern (see Papini 2003 for a comparative review of surprising reward omission effects).

To our knowledge, no positive demonstration of SNC exists in birds. To account for the absence of demonstrated SNC in nonmammalian vertebrates, some authors have proposed that this may reflect a real performance dissimilarity between taxa, and could be an expression of evolutionary divergence in the mechanisms dealing with surprising negative changes in reinforcement (Bitterman 1975; Papini 1997, 2003). From a functional point of view, this interpretation implicitly posits that the putative advantages that led to the evolution of SNC in mammals either were not present in the other taxa or require cognitive resources not available to them. We find both suggestions unconvincing for the following reasons: (1) birds have shown ability to be influenced by expectations during operant tasks (e.g. starlings in Kacelnik et al. 1987, and pigeons in Clement & Zentall 2002) which is a cognitive prerequisite to express SNC; and (2) there exist other commonalities between the behaviour of birds and mammals during unexpected reward omissions that favour the view that SNC should be present in birds. For instance, authors commonly interpret SNC as being partly the consequence of an aversive reaction triggered by a significant reward loss (e.g. Amsel 1992; Flaherty et al. 1998). Birds do show aversive responses during surprising nonreinforcement as has been shown in pigeons which increase their aggression towards another pigeon in the extinction phase of an operant task (Azrin et al. 1966), and learn to peck an 'escape from S−' key during the initial sessions of an S+/S− discrimination task (Terrace 1971).

As an alternative to the evolutionary divergence hypothesis, the reported absence of SNC in nonmammals may have resulted from failures of detection because of methodological differences across studies. Many parameters affect SNC in mammals (e.g. food deprivation level, the length of the interval between phases, the discrepancy between the reinforcers involved, etc.; Flaherty 1996, pp. 19–53), and knowledge about these effects comes mainly from studies with laboratory rats. Extrapolation of these dependencies to other species is far from simple given major differences in, for example, energetic requirements, metabolism and perceptual systems. Even in rats, successive contrast effects have proved difficult to observe in some situations (e.g. instrumental SNC in rats has been elusive when the reinforcers used are sucrose solutions, although consummatory SNC with the same solutions is a common finding; Flaherty 1996, page 51).

Our main goal in this study was to test the hypothesis that, in spite of previous negative results, SNC should occur in a bird, and we used the European starling, *Sturnus vulgaris*, for this primary objective. Furthermore, and conditional to success in the latter, we wished to start exploring functional dimensions of SNC by more detailed scrutiny of its behavioural expressions and its relation to the information status of the subject.

In experiment 1, we used a procedure that allowed recording of consummatory and instrumental behaviours and had several elements in common with a design where rats had a richer range of behavioural opportunities than in the canonical tests (Pecoraro et al. 1999, experiment 1). In this experiment, the rats evidenced consummatory SNC, elevated activity and increased exploration during a surprising reward reduction (for further details see the introduction to experiment 1 below).

Our experimental design had two novel features in respect to previous attempts to find SNC in birds. First, we measured consummatory behaviour, which is thought to be more sensitive to changes in reward parameters than instrumental responses (Flaherty 1996, page 53) and second, instead of producing the downwards shift by varying the amount of reinforcer provided, as in Papini's (1997) experiment with pigeons, we manipulated the quality of incentives from the preshift to the postshift phase using foodstuffs of different palatability, as this is more immediately discriminable than reward amount.

Our second goal was to address the functional consequences of SNC. The set of responses usually found during SNC is worth functional analysis because it is pervasive across the mammalian spectrum, in spite of causing immediate energy and time costs. When circumstances deteriorate, animals showing SNC partially suppress consumption and increase their general activity relative to controls. These are costs that should be compensated for by some correlated gains which have not yet been explored.

According to the functional-search hypothesis (Pecoraro et al. 1999), the detection of a significantly less than expected reinforcer causes a change in motivational modes from consumption to exploration. Briefly, Pecoraro et al. (1999) argued that consummatory suppression and increased searching behaviour during a surprising reward reduction are two sides of the same underlying process of feeding regulation. This psychological suggestion matches ideas developed in the behavioural ecological literature on patch exploitation. For instance, Bernstein et al. (1988, pp. 1019–1020) built consumer-distribution models that assumed that predators formed expectations about patch quality using simple learning rules, and then applied a criterion for either continuing to consume food in the present patch (when yield equals or exceeds expectation) or switching to sampling the environment (when yield is below expectation). Thus, this type of functional ecological model also predicts that downshifted animals should reduce consumption and increase exploration compared to conspecifics that have been in a poor environment throughout, and hence have an expectation that matches the experienced yield. This functional analysis of SNC offers a good chance of further integration of psychological and ecological models of behaviour.

The functional-search hypothesis, we believe, implicitly assumes that the cost of suppressing consumption during SNC is outweighed by the potential benefits of finding richer alternatives through increased exploration. When a source of reward goes dead, the greater its preshift value, the more searching increases, and this implies lower exploitation of the impoverished (postshift) available opportunities. This is close to the optimal sampling ideas in the foraging literature (e.g. Stephens & Krebs 1986, page 81). Increased sampling after a greater loss can lead to higher overall gain rates even if it has an immediate exploitation cost, depending on the assumptions about the frequency of changes and the distribution of food sources in the habitat. The conflict between exploration and exploitation has been a prevalent interest in the foraging literature for a long time (e.g. Krebs et al. 1978; Stephens & Krebs 1986). Qualitatively, the balance may be positive if exploration during the depressed foraging period caused by SNC is on average successful in

finding an alternative source of reinforcement that is sufficiently better than the rejected lower incentive to pay for the loss in exploitation benefits. As various optimal foraging models demonstrate (e.g. Stephens & Krebs 1986, page 81), this in turn depends on the stability and variance of the environment in question and the information the animal has about it. For instance, subjects should benefit less by sampling the greater the information they possess about the preshift and postshift environments.

Animals provided with information about the environmental state should be able to reduce costly sampling behaviour compared to that shown by uninformed subjects during SNC. Just as greater preshift value counterintuitively predicts faster abandonment of the previously richer source, greater preshift information should facilitate the detection of a change and then reduce the consumption suppression typical of SNC. To our knowledge, these issues have not hitherto been tested in any species. In our second experiment we dealt with this problem experimentally, by using an SNC-related paradigm with different degrees of information.

EXPERIMENT 1

Experiment 1 is an adaptation of the procedure of Pecoraro et al.'s (1999) experiment 1 with rats. We were inspired by their procedure, first, in presenting a consummatory SNC situation, and second, in allowing subjects to explore many feeders and to move around in a larger arena than commonly used in SNC procedures. In their experiment, the preshift phase consisted of rats gaining access to a sucrose solution from a drinking bottle located in one of the arms of a four-armed radial maze, while empty drinking bottles were present in the three remaining arms. Rats from the control group received a less preferred 4% sucrose solution, and subjects from the contrast group received a highly preferred 32% sucrose solution. In the postshift phase, rats of both treatments received only the lower sucrose concentration which was present in drinking tubes of all arms of the apparatus. After the shift, the rats in the 32% group presented consummatory SNC (drank less sucrose solution), increased general activity and augmented exploration compared with rats in the 4% group that had always had the 4% solution (Pecoraro et al. 1999). Our first experiment aimed at testing whether starlings during such an SNC procedure show behaviour similar to that shown by rats.

Starlings were randomly assigned to two groups, 'contrast' and 'control' ($N = 9$ each), and each experienced 15 preshift sessions where three identical food bowls were presented. One bowl was baited (the focal feeder) and the other two were empty. The focal feeder in treatment contrast contained a highly preferred food (mealworms), whereas in treatment control it contained a much less preferred food (turkey crumbs). The day after the preshift phase finished, starlings from both treatments were unpredictably exposed to all three feeders filled with the less preferred food for another nine sessions (postshift phase). Hence, our procedure allowed for a qualitative comparison between starlings' and rats' behaviour in a similar set-up.

In addition, if a frustration-like mechanism were involved during the SNC, so that a negative effect becomes associated with the focal feeder where the unexpected absence of a favoured reinforcer is experienced (i.e. conditioned frustration; Amsel 1992), after the downward shift that focal feeder should receive less foraging behaviour than the alternatives.

Methods

Subjects

We used 18 wild-caught starlings (under licence from Natural England). They were caught in Walton upon Thames, near London,

U.K. using whoosh nets. Although age was unknown at the time of capture they were all at least 1.5 years old at the time of the experiment. Recently captured birds were released in large communal aviaries (4.4 × 2.3 m and 2.1 m high) with a translucent roof. Bird density was kept below 1 bird/m³. The aviaries contained many perches, sand trays for enrichment and water pools (50 × 40 cm and 15 cm deep). There was permanent ad libitum access to food (a mixture of mealworms, Tenebrio sp., turkey crumbs, Orlux Remiline universal granules) and fresh drinking water. All birds spent a minimum of 40 days in communal aviaries before participating in any experiment. Before the present experiment started, subjects had already spent a year in captivity and had accumulated similar experimental experience in pecking at lit keys to obtain food (precision pellets).

For the present experiment, starlings were transferred to indoor individual cages that served as housing and experimental chambers where subjects were visually but not acoustically isolated. These indoor cages were stacked in groups of three, one above the other, in climate-controlled rooms maintained at 16 °C (±3 °C). Automatic timers maintained a light:dark cycle of 12:12 h (lights on at 0700 and off at 1900 hours). For enriching purposes, 10 × 10 cm mirrors were hung within each cage during nonexperimental hours (starlings are normally social, and they often approached and spent time close to these mirrors, receiving visual stimulation similar to that received from conspecifics), and bathing pools were provided twice a week on afternoons once the experimental session was over. Fresh drinking water was always available, and access to food was permitted at least 1 h after the end of the last experimental session for a period of 3 h. Those birds that had access to mealworms during experimental sessions were allowed to feed ad libitum on turkey crumbs and Orlux granules; and those birds that had access to turkey crumbs during experimental sessions were allowed to feed ad libitum on mealworms and Orlux granules (this regime applied during both preshift and postshift phases). This feeding regime allowed: (1) a food deprivation period of approximately 15 h between days; (2) the starlings to maintain their body weights at or above 90% of their free-feeding values; and (3) subjects from different experimental treatments to experience equally balanced diets, which resulted in statistically nondifferent mean body weights and relative weight losses across conditions. There remains a possibility that starlings might show a partial rather than absolute preference for mealworms over turkey crumbs, if they were exposed for a long time to both foodstuffs. This however, is not relevant to our experiments, as we conducted the experiments under open economy regimes and, within our timescales, we observed absolute preference for live prey.

The experiment took place from December 2006 to January 2007. The following spring, we released all starlings from Oxford University Wytham Field Station after checking their condition. Before release they were kept in an outdoor aviary with food ad libitum for 2 weeks. Experimental procedures were approved by the ethical review board at the Zoology Department, University of Oxford.

Apparatus

Each experimental cage measured 158 × 56 cm and 53 cm high, and had two perches (85 cm apart). To present food during experimental sessions, we used cylindrical ceramic bowls, 7 cm in diameter and 5 cm in height, that were covered with a circular surface made of black EVA (ethylene vinyl acetate) foam. These lids were intended to obstruct the view of the content of the bowls, although each lid had an X-shaped cut that let starlings peck through and get the food in the container. We filmed subjects during test sessions with two camcorders: a Canon MVX460 and a Sharp VL-E685U.

Procedure

Pretraining. Animals were pretrained to eat from ceramic bowls covered by an EVA foam surface with an X-shaped cut. This took at most 5 days after which the preshift phase began.

Preshift phase. Before the preshift phase, the 18 subjects were matched-paired based on pretraining weight (to homogenize treatments) and then randomly separated into two independent groups: contrast ($N = 9$) and control ($N = 9$) conditions. The preshift phase consisted of 15 sessions of 10 min each, administered at a rate of three sessions per day, starting at 0930, 1100 and 1230 hours. Starlings were trained in squads of three birds, and the order of squads was rotated across days. For a particular bird, a session started when the experimenter placed three covered bowls in the cage, two at the extremes and one in the middle. Two of those bowls were always empty, and the third one (the focal feeder) had mealworms (preferred food) for animals in the contrast condition or turkey crumbs (less preferred food) for animals in the control group. Bowls were filled with approximately 14 cm^3 of food each. For a particular bird, the focal feeder was always in the same position (either on the right or the left side of the cage), but right and left positions were counterbalanced across subjects. A session finished after 10 min, when the experimenter removed all three feeders.

Postshift phase. The day after the 15th preshift session was completed, the postshift phase began. In this phase, starlings experienced nine 10 min sessions across 3 days (i.e. three sessions per day). Each session was similar for both groups, with all three feeders covered by a foam lid and filled with turkey crumbs. Therefore, starlings in the contrast condition experienced a reward downshift from a preferred food (mealworms) in one feeder to a less preferred food (turkey crumbs) in all three feeders. Birds in the control condition received the same reinforcer they were used to eating in the preshift phase (turkey crumbs), but postshift all three bowls had turkey crumbs, instead of only one. The amount of food available in a session (both in preshift and postshift phases) was always enough to make it impossible for a starling to empty the bowls in 10 min. Thus, conditions for the control group remained mostly unchanged across phases, except for the fact that turkey crumbs could be found in more feeders in postshift sessions.

Dependent measures. We registered the amount (g) of food consumed per session as the main dependent measure across both preshift and postshift phases. To compare the amounts of food consumed, we multiplied the weight (g) of mealworms by 0.45, assuming that Tenebrio sp. larvae contain approximately 55% of water (see e.g. Hope et al. 1999; turkey crumbs have negligible water content). We filmed starlings during the last three sessions of the preshift phase and the first three sessions of the postshift phase. Two observers, who were uninformed of the subjects' group assignment, watched the videos and registered the following mutually incompatible behavioural events: walking, flying and feeder probing (i.e. each time the subject inserted its beak through the X-shaped cut of a bowl cover, also registering from which feeder the subject was probing). These events were sampled once a second using JWatcher software (Blumstein et al. 2006), and, thus, a total of 600 events was recorded per 10 min session. We also calculated the number of switches between feeders, which we used as a measure of exploration. Interobserver reliability (agreements/total observations) was above 90%.

Conventional ANOVAs with two independent groups (i.e. contrast and control conditions) were done on weight of dry food consumed in both preshift and postshift phases, including sessions as repeated measures. Analyses of variance were also done with general activity (i.e. walking + flying), feeder probing and exploratory behaviour (i.e. feeder switching). The value of α was set at 0.05.

Results

Consumption

Figure 1 shows the main consummatory results of both preshift and postshift phases for control and contrast treatments. During the preshift phase, subjects in both groups consumed progressively more of their corresponding foodstuff (mealworms in the contrast and turkey crumbs in the control group) across sessions. The mealworm-eating birds (contrast group), however, reached a consumption asymptote reliably above that of the control subjects. The statistical analysis of weight of dry food consumed in the 15 preshift sessions showed a significant effect of treatment (ANOVA: $F_{1,16} = 20.73$, $P < 0.001$), session ($F_{14,224} = 15.66$, $P < 0.001$) and treatment*session interaction ($F_{14,224} = 3.07$, $P < 0.001$).

Despite treatments differing in mean asymptotic consumption, there was no treatment effect on the number of probing events (i.e. number of beak insertions) in the focal feeder during the last three
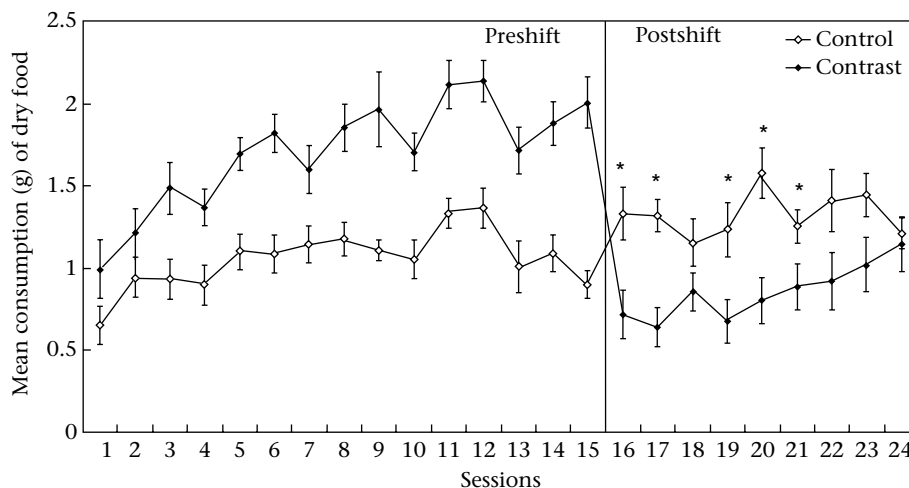

Figure 1. Experiment 1. Consumption of dry food as a function of session and treatment. Starlings in the contrast group had access to mealworms (preferred) during the preshift phase, and only turkey crumbs during the postshift phase, while controls had access only to turkey crumbs in both phases. Error bars denote ±1 SEM; *$P < 0.05$.

preshift sessions: treatment, session and treatment*session interaction (ANOVA: all $Fs < 1$).

As shown in Fig. 1, starlings from the contrast group responded to the change from mealworms to turkey crumbs with a sharp decline in weight of dry food consumed; their consumption was significantly lower than that of the control subjects in five of the first six postshift sessions. As the postshift phase progressed, however, contrast subjects approached the controls' level of consumption. An analysis of consumption for all nine postshift sessions showed a significant treatment effect (ANOVA: $F_{1,16} = 8.76$, $P < 0.01$), a significant session effect ($F_{8,128} = 2.51$, $P < 0.05$) and a significant treatment*session interaction ($F_{8,128} = 2.75$, $P < 0.01$).

During postshift, controls encountered the two previously (preshift) empty bowls baited with turkey crumbs. To test the possibility that the experience of a positive upshift by controls could have determined the significant difference in consumption between controls and subjects from the contrast group during the postshift phase, we made two comparisons. First, if the controls' postshift positive contrast had been the determinant of postshift consummatory differences between treatments, we would expect to observe no reliable negative contrast when comparing the contrast group's mean postshift consumption with the controls' mean consumption during preshift (where no upshift had happened yet). When we compared mean weight consumed during the first six postshift sessions of contrast subjects and the mean consumption of the last six preshift sessions of controls, an SNC was still evident by contrast subjects presenting a reliable lower consumption of turkey crumbs ($\overline{X} \pm 1$ SEM $= 0.76 \pm 0.1$ g) relative to controls (1.13 ± 0.08 g; $F_{1,16} = 7.74$, $P = 0.013$). Second, when we compared the controls' mean consumption in the postshift phase and their own consumption in a comparable number of sessions of the preshift phase (i.e. the last nine preshift sessions), we found no reliable effect of phase ($F_{1,8} = 2.84$, $P = 0.13$), which suggests that the controls' consumption remained more or less stable across phases and this does not support the idea of a positive contrast having occurred.

General activity

Figure 2 shows the main results regarding the starlings' behavioural records during the last preshift and first postshift sessions. Control animals in the preshift phase were similarly active as contrast subjects, and then kept those levels of activity unchanged during the postshift phase. However, starlings in the
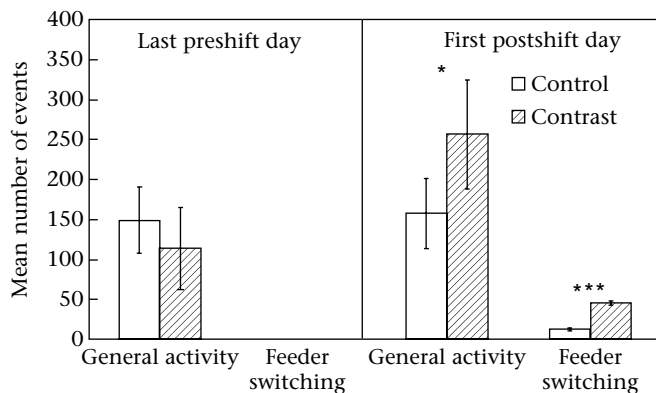
contrast group augmented their level of general activity (i.e. walking + flying) from the preshift to the postshift phase. The ANOVA with treatment and phase (in this analysis, the 'preshift phase' score was the sum of scores of the last three preshift sessions, while the 'postshift phase' score was the sum of scores of the first three postshift sessions) as factors showed a nonsignificant main effect of treatment (ANOVA: $F_{1,16} = 0.18$), a significant main effect of phase ($F_{1,16} = 27.78$, $P < 0.001$) and a significant treatment*phase interaction ($F_{1,16} = 21.61$, $P < 0.001$).

Exploration

Feeder switching or exploration was negligible during the preshift phase as starlings from both conditions learned to avoid empty feeders and only approached the focal one (i.e. the feeder containing food). In the postshift phase, contrast subjects increased searching. On the first day of the postshift phase (including the sum of the scores obtained in the three sessions of that day for each subject) contrast group subjects showed more switching events ($\overline{X} \pm 1$ SEM $= 45.67 \pm 2$) than subjects in the control group (12.89 ± 2), and this was statistically significant (treatment, ANOVA: $F_{1,16} = 107$, $P < 0.001$).

Although birds in the contrast treatment ate less of the turkey crumbs in the first postshift day than control starlings, both groups showed approximately the same amount of probing behaviour from the focal feeder, and this score remained mostly unchanged between phases for both groups. An ANOVA with treatment and phase as factors showed a nonsignificant main effect of treatment ($F_{1,16} = 0.22$), a nonsignificant main effect of phase ($F_{1,16} = 2.45$) and a nonsignificant treatment*phase interaction ($F_{1,16} = 0.77$). It could be argued that the present 'probing response' or beak insertion behaviourally resembles 'key pecking' more closely than actual 'consummatory' responses. Unlike our results using consumption, starlings' probing behaviour showed the same lack of evidence for SNC as has been reported using key pecking in pigeons (see Papini 1997, experiment 2).

Finally, to explore predictions from Amsel's frustration theory (see introduction to experiment 1), we computed the proportion of the amount eaten from the focal feeder across postshift sessions. Because there were three baited feeders during the postshift phase, the chance expectation was one-third. Nevertheless, both groups presented a mean ± 1 SEM proportion of consumption from the focal feeder highly above the 0.33 indifference point (contrast group: 0.59 ± 0.08; control group: 0.77 ± 0.06). The analysis with treatment and postshift session as factors showed no effect of treatment (ANOVA: $F_{1,16} = 2.88$), session ($F_{8,128} = 1.23$) or treatment*session interaction ($F_{8,128} = 0.54$).

Discussion

Our results thus support the presence of consummatory SNC in starlings. To our knowledge, this is the first report of SNC in a bird species (for reviews on different aspects of surprising reward changes, see Flaherty 1996; Papini & Dudley 1997; Papini 2003).

Contrast birds showed consummatory suppression, increased general activity (i.e. walking and flying) and more searching behaviour (i.e. feeder switching) relative to controls during the first few sessions of the postshift phase, as predicted by Amsel's (1992) frustration theory, by the functional-search hypothesis (Pecoraro et al. 1999) and by ecological models of patch exploration–exploitation (Bernstein et al. 1988). Frustration theory also predicted that the area or feeder where frustration could have been triggered might become aversive by being associated with a negative experience (i.e. primary frustration), and thus be avoided by the animal. However, birds that experienced the negative contrast in our

Figure 2. Experiment 1. General activity and exploration (feeder switching) split by experimental phase and treatment (the score for each subject is the sum of its scores for the three sessions preceding and following the shift). General activity was a composite score that included walking and flying events. Switching events indicate changes from probing on one feeder to probing on another. Error bars denote ± 1 SEM; *$P < 0.05$; ***$P < 0.001$.

experiment did not appear to develop an aversion towards the focal feeder from which mealworms were removed. Downshifted birds probed from the focal feeder similarly to controls and ate mostly from there.

Overall, results from the present experiment may stimulate re-evaluation of the idea that there is a substantial difference between mammals and birds in the mechanisms responsible for phenomena such as SNC. Our procedure was very similar to Pecoraro et al.'s (1999) experiment 1 with rats, and the results of both experiments closely resemble each other in important respects. First, both rats and starlings presented consummatory SNC when the preferred reinforcer was suddenly replaced by a poorer one. Second, subjects in both species increased general activity and exploratory behaviours after the shift. Third, and in contrast to predictions from Amsel's (1992) frustration theory, neither rats nor starlings appeared to develop an aversion towards the feeder where the higher reinforcer was missing. We also acknowledge that behavioural similarities do not necessarily involve similarity in the underlying mechanisms, and, therefore, these issues would gain important insight from further behavioural, brain and neurochemical comparative studies of SNC in birds and mammals.

In short, according to this evidence, it seems parsimonious to interpret the results as rats and starlings presenting similar behavioural patterns under similar changes in foraging opportunities, rather than showing the consequences of a phylogenetic history of divergent nonadaptive mechanisms.

Interesting functional aspects of the conflict between exploration and exploitation (consumption) remain unexplained. For instance, it might first be thought that consummatory suppression is just a by-product of time constraints, in which case an increase in exploration simply steals time available for consumption. However, our results show that this is not the case. Our birds spent less than 40% (on average) of postshift sessions walking, flying and probing from feeders, spending most of the time sitting on perches or on the cage floor. Hence, exploration time did not physically limit the opportunity for turkey crumb consumption. If not liberating time for exploration, why did starlings suppress consumption during the postshift phase? We do not know, but the flavour of this puzzle is similar to issues raised in an earlier study of time allocation between costly (flying-dependent) and cheap (walk-dependent) foraging modes. As here, in such a situation starlings spent most of their time inactive, but when they did forage their behavioural allocation between foraging modes maximized the net rate of energy gain (Bautista et al. 2001).

EXPERIMENT 2

Efficient foragers should be sensitive to the overall foraging opportunities in the environment (e.g. Charnov 1976a, b), to the extent that they have information about it. If an animal gives up a source of food to invest time searching for better alternatives, environmental information relative to the available opportunities could be crucial (e.g. Charnov 1976b; Freidin 2007). Thus, an animal that has more information regarding cues about the absence of richer options should show less exploration and less rejection of poorer alternatives relative to a less well-informed individual. We designed experiment 2 to investigate this idea.

Methods

Subjects and apparatus

We used 20 experimentally naïve starlings caught and kept under similar conditions as those described for experiment 1.

The experiment took place during January and February 2007. After the experiment finished, the birds were kept for further

research. Experimental procedures were approved by the local ethical review board at the Zoology Department, University of Oxford.

Procedure

Pretraining. This phase was as described for experiment 1 and once finished was followed by the preshift phase on the next day.

Preshift phase. Before the preshift phase and to homogenize experimental groups, subjects were matched-paired based on pretraining weight and then a member of each pair was randomly assigned to either group. The preshift phase consisted of 18 sessions presented at a rate of three sessions per day. Daily times of sessions were similar to those reported for experiment 1, but sessions lasted 5 instead of 10 min. For both treatments, a session started when the experimenter placed four covered bowls in the cage, one in each corner. One bowl contained mealworms, while the remaining three contained turkey crumbs. During preshift sessions, birds experienced three feeders with the lid of the same colour, and a fourth one with an odd-coloured lid. For starlings in treatment cued, the colour of the lid signalled the kind of food inside the bowl: the odd-coloured lid identified the bowl containing mealworms. In treatment uncued, the odd-coloured lid was randomly assigned to either a mealworm or a turkey crumb feeder on every session; hence lid colour was uninformative. Lids could be either yellow or orange, and which one was the odd colour was counterbalanced across animals. Moreover, the corner where the bowl with mealworms was placed was randomly changed across sessions in both treatments so that birds could not use spatial information to find their preferred food.

Postshift phase. The postshift phase began the day after the preshift phase was over, and lasted for six sessions at a rate of three per day. A postshift session started when the experimenter placed four bowls in the bird's cage. In contrast with preshift sessions, all four feeders contained turkey crumbs. Hence, subjects in both treatments experienced the absence of their preferred reward. During the postshift phase, all four cover lids had the same colour (the colour that appeared in three of the four feeders during the preshift phase). For subjects in treatment cued, that colour was associated with turkey crumbs. Therefore, starlings in treatment cued could detect the absence of the signal for mealworms in the postshift environment without probing, while uncued starlings could not.

Dependent measures. We recorded the amount of mealworms and turkey crumbs consumed and the number of turkey crumb feeder probing events during sessions of both preshift and postshift phases. The last three preshift sessions and the first three postshift sessions were filmed. Two observers uninformed of the subjects' group assignment watched the videos and used JWatcher software (Blumstein et al. 2006) to register the following mutually incompatible behaviours at a rate of one per second: walking, flying and feeder probing (including from which feeder the bird was probing). A total of 300 events was recorded per 5 min session. We also calculated the number of switches between feeders, which we used as a measure of exploration. Interobserver reliability was above 90% (i.e. agreements/total observations). Statistical procedures were similar to those described for experiment 1.

Results

Consumption

Figure 3 presents the amount of dry food consumed during preshift and postshift sessions. Consumption of turkey crumbs in the preshift phase was negligible for both treatments. As seen in
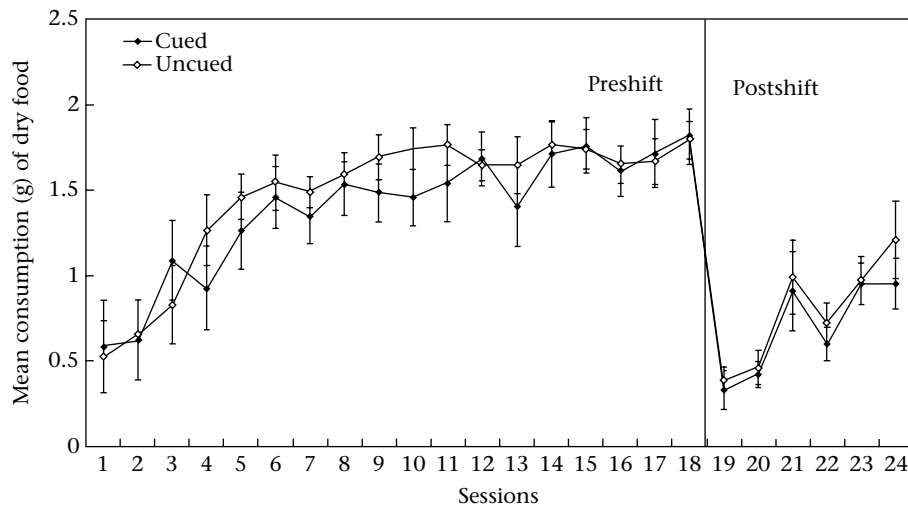
Figure 3. Experiment 2. Consumption of dry food as a function of session and treatment. Starlings in both treatments had access to one bowl of mealworms and three of turkey crumbs during the preshift phase, but only four bowls of turkey crumbs during the postshift phase. In treatment cued, the feeder containing mealworms before the shift was colour coded, while in treatment uncued it was not. Error bars denote ±1 SEM.

Fig. 3, starlings from both conditions similarly increased their mealworm intake across preshift sessions, which was also reflected in the analysis of the 18 preshift sessions (session, ANOVA: $F_{17,306} = 22.09$, $P < 0.001$; treatment and treatment*session interaction: both $Fs < 1$). Moreover, starlings from both treatments reached a similar level of asymptotic consumption of mealworms during the preshift phase. The analysis of the last nine preshift sessions showed no significant effect of treatment (ANOVA: $F_{1,18} = 0.18$), session ($F_{8,144} = 1.83$, $P = 0.08$) or treatment*session interaction ($F_{8,144} = 1.15$).

Figure 3 also shows that in the postshift phase both groups had a sharp drop in weight of turkey crumbs consumed relative to their level of mealworm consumption in the previous phase. An analysis of dry food consumed with the last preshift day and the first postshift day as repeated measures showed a significant effect of phase (ANOVA: $F_{1,18} = 182$, $P < 0.001$) and no effect of treatment or treatment*phase interaction (both $Fs < 1$). The amount of food in each bowl during both preshift and postshift phases was such that subjects could not finish it within a session, and, hence, consumption could not have been affected by food depletion. In addition, the amount of turkey crumbs eaten increased for both treatments across postshift sessions, which was confirmed by a reliable effect of session (ANOVA: $F_{5,90} = 11.8$, $P < 0.001$) and no significant effect of treatment or treatment*session interaction (both $Fs < 1$).

General activity

There was no reliable effect of treatment on general activity (a composite score of walking and flying events) for the last three sessions of the preshift phase (treatment, session and treatment*session interaction, ANOVA: all $Fs < 1$). Birds in both treatments increased their general activity on the first postshift day relative to the last preshift day (the score for a day is the sum of scores of the three sessions on that day; Fig. 4). Mean ± 1 SEM preshift activity was 38.5 ± 11 and 57.5 ± 20 activity events for treatments cued and uncued, respectively, while mean postshift activity events were 101.5 ± 12 and 134.3 ± 19 for treatments cued and uncued, respectively. The analysis revealed a significant effect of phase (ANOVA: $F_{1,18} = 51.25$, $P < 0.001$), but no reliable effect of treatment ($F_{1,18} = 1.59$, NS) or treatment*phase interaction ($F < 1$). Moreover, all starlings decreased their activity levels as sessions progressed on the first postshift day; that was confirmed by a significant effect of

session (ANOVA: $F_{2,36} = 8$, $P < 0.01$), and no reliable effect of treatment ($F_{1,18} = 1.18$, NS) or treatment*session interaction ($F < 1$).

Exploration

As the preshift phase progressed, subjects in both treatments learned to avoid visiting turkey crumb feeders (Fig. 5). The analysis of probing behaviour towards turkey crumb feeders as a function of treatment and preshift day (i.e. block of three sessions) only showed a significant effect of day (ANOVA: day: $F_{5,90} = 11.2$, $P < 0.001$; treatment and treatment*day interaction: both $Fs \leq 1$). Starlings in treatment cued, however, reached an asymptotic level of probing into turkey crumb feeders significantly below that of uncued subjects. The analysis of the last 4 days of the preshift phase presented a significant effect of treatment (ANOVA: $F_{1,18} = 14.69$, $P < 0.01$) and day ($F_{3,54} = 8.42$, $P < 0.001$), although no effect of treatment*day interaction ($F < 1$). On the last preshift day, cued subjects presented a mean ± 1 SEM of 1.3 ± 0.7 turkey crumb probing events against a mean of 8.7 ± 1.8 of subjects in treatment uncued; data were transformed for analysis into 'log (score + 1)' to obtain homogeneity of variance (Bartlett test: $\chi_1^2 = 0.99$, $P > 0.1$) and the analysis confirmed a significant difference between
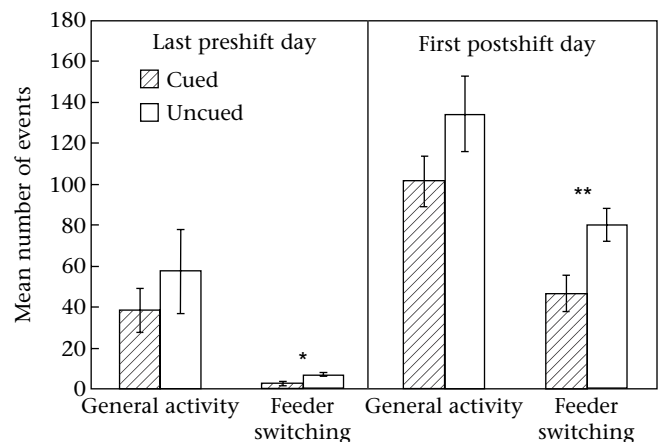

Figure 4. Experiment 2. General activity and exploration (feeder switching) recorded as in Fig. 1 and split by experimental phase and treatment. Error bars denote ±1 SEM; *$P < 0.05$; **$P < 0.01$.
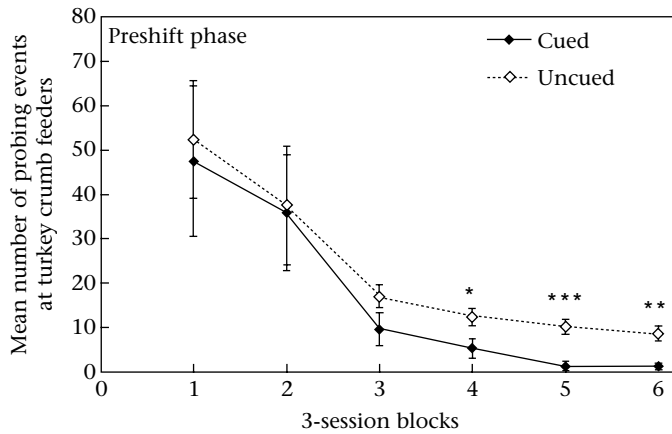
Figure 5. Experiment 2. Probing at turkey crumb feeders as a function of treatment and block of sessions in the preshift phase. Error bars denote ±1 SEM; *P < 0.05; **P < 0.01; ***P < 0.001.

Figure 6. Experiment 2. Feeder-switching events (exploration) as a function of treatment and session in both preshift and postshift phases. Error bars denote ±1 SEM; *P < 0.05; **P < 0.01.

treatments (ANOVA: $F_{1,18} = 30.35$, $P < 0.001$). In terms of mean feeder-switching events on the last preshift day (Fig. 4), cued starlings presented a mean ± 1 SEM of 2.6 ± 1.1, which was significantly below the 7.1 ± 0.9 mean score of subjects in treatment uncued (ANOVA: $F_{1,18} = 9.14$, $P < 0.01$).

Once in the postshift phase, both groups of starlings significantly increased exploratory behaviours as shown by their feeder-switching events (Fig. 4). The amount of postshift switching was higher for uncued than to cued birds ($\overline{X} \pm 1$ SEM $= 80 \pm 8$ and 47 ± 8 switching events on the first postshift day, respectively). The analysis of switching events with last preshift and first postshift days as a within-subject factor showed a significant effect of treatment (ANOVA: $F_{1,18} = 8.97$, $P < 0.01$), a reliable phase effect ($F_{1,18} = 106.36$, $P < 0.001$) and a significant effect of treatment*-phase interaction ($F_{1,18} = 6.52$, $P < 0.05$). The significant phase*-treatment interaction suggests that the shift between phases differentially affected the treatments' change in exploratory behaviour.

Postshift feeder-switching scores started higher for treatment uncued relative to treatment cued, although both groups decreased their searching behaviour across postshift sessions, and eventually reached a similar performance by the end of the postshift phase (Fig. 6). The analysis of switching scores for all six postshift sessions presented a main effect of treatment (ANOVA: $F_{1,18} = 6.29$, $P < 0.05$), a reliable effect of session ($F_{5,90} = 43.52$, $P < 0.001$) and a significant treatment*session interaction ($F_{5,90} = 7.05$, $P < 0.001$). The analysis of switching behaviour for each individual postshift session showed a significant effect of treatment for early sessions, declining towards the end of the experiment (Fig. 6). In short, starlings in treatment uncued explored significantly more than birds in treatment cued in the early postshift sessions, but the difference between groups declined as the birds settled in the new environment.

Discussion

Similarly to the SNC observed in group contrast in experiment 1, in experiment 2 once the preferred food was omitted starlings dropped consumption below preshift levels, and then recovered across the postshift phase. Consummatory suppression and increments in general activity during the postshift phase were not affected by the differential information between groups acquired during the preshift phase. Searching (exploratory probing), however, was lower at the beginning of the postshift phase for informed relative to uninformed birds.
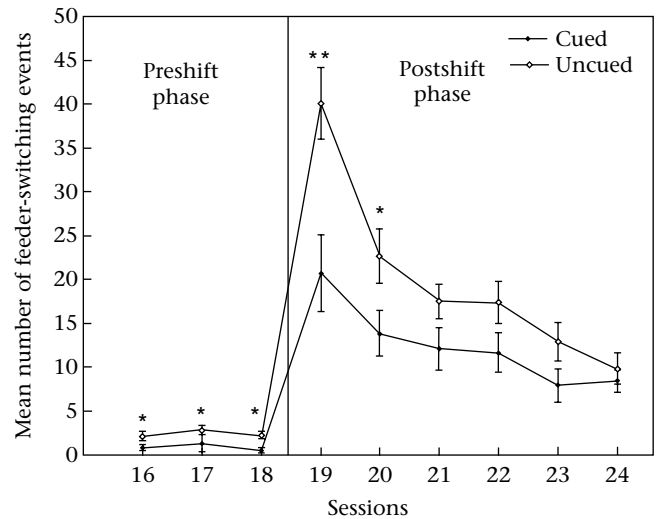
Cued animals already showed lower sampling in the preshift phase, but this difference does not explain the postshift differences, as animals from both groups increased their exploration scores from preshift to postshift by a factor of 10 or more, and a significant phase*treatment interaction implies that the shift affected the treatments' change in exploration across phases differently. In addition, exploration scores in the preshift phase were minimal for both groups, and were differentially constrained by the speed at which starlings could find the mealworms (starlings in treatment cued directly approached the mealworm feeder by the end of the preshift phase). While the discovery of mealworms ended sampling preshift, in the postshift phase there were no mealworms to be found, and hence the birds could continue to search indefinitely.

While the predicted reduction in sampling as a function of information was confirmed, some aspects of the results are not functionally obvious. Informed birds showed similar suppressed consumption and increased general activity to that of their uninformed counterparts, thus failing to reap any benefits from their information other than the reduction in sampling. Of course, should sampling be truly costly, this may be a sufficient advantage.

The dissociation in susceptibility to acquired information of consumption and general activity versus exploration implies that these responses did not work as a functional unit as the functional-search hypothesis suggests (Pecoraro et al. 1999).

GENERAL DISCUSSION

In experiment 1, we showed for the first time that individuals from a bird species (European starlings) display consummatory SNC and increase general activity and exploration when a preferred foodstuff is omitted, as had been previously reported in mammals (e.g. Flaherty et al. 1978; Pecoraro et al. 1999; Freidin et al., 2005). The starling results resemble those obtained with rats in a similar procedure (experiment 1 in Pecoraro et al. 1999), thus suggesting that, in contrast to the idea of a deep evolutionary divergence between birds and mammals in terms of the psychological mechanisms involved during surprising negative changes in reward conditions (see Papini 2003, and discussion of experiment 1 above), both taxa may respond to a universal problem during natural

foraging by either converging to the same mechanisms or preserving ancestral response patterns.

In experiment 2, we tested and confirmed the hypothesis that if the increment in exploratory behaviour accompanying SNC was related to adaptive sampling, then animals that already possess more information should show a lesser increment when their preferred food is absent. As expected, starlings that could visually determine the absence of preferred food explored significantly less than those that did not possess the same information. Against our expectation, however, this did not translate into any measurable advantage in the conditions of the test, as birds in both treatments suppressed consumption similarly and had almost identical mean scores of general activity. It remains possible, however, that the functional suppression of sampling is of much greater benefit under more demanding natural circumstances.

The integration of psychological and functional perspectives is often predicated but less often implemented experimentally. The present study shows one case in which the integration inspired the question and nourished the interpretation. We are far from understanding the full impact on the subjects' previous expectations on their current foraging. However, as more detailed knowledge accumulates, we expect to clarify the role played by natural selection and phylogenetic constraints on the evolution of the mechanisms involved in animal responding to reward fluctuations.

Acknowledgments

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