Deprivation of direct adult contact during development affects social representation in a songbird

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Deprivation of direct adult contact during development affects social representation in a songbird

Short title: social cognition development in birds

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Abstract

Social cognition involves a wide array of skills which are built largely through interactions with conspecifics and therefore depend upon early social experience. Motivation for social stimuli is a key feature of social behaviour and an operant conditioning task showed that isolated wild-caught adult starlings (*Sturnus vulgaris*) are highly motivated to access pictures of other starlings. Here we show that hand-raised adult starlings maintained in groups of peers throughout development but without any contact with adult models were not or only poorly motivated to access pictures of conspecifics. Moreover, they did not prefer pictures of starlings to pictures of landscapes, unlike birds wild-caught as adults. These results raise questions about the role of social experience during development, particularly with adult models, in the development of social motivation and of social representation in general.

Keywords: social deprivation, social motivation, social representation, social cognition, adult influences, operant conditioning

Introduction

Social cognition refers to abilities such as perception, learning or memory that enable individuals to organize interactions with conspecifics (Frith, 2008). Adults' cognitive traits are influenced by conditions experienced during early development (Nettle et al., 2015). The importance of bi-directional interactions between social environment and cognitive performance is well known (Boogert et al., 2018). Social skills develop from experiential learning with other individuals (Hesse & Thünken, 2014). Social deprivation during development is thus associated with a wide range of long-term defects such as increased aggressiveness (Tóth et al., 2008; Halperin & Dunham, 1993), social withdrawal (Bouet et al., 2010), or anxiety (Ros-Simo & Valverde, 2012). In particular, the presence of parents is important: juvenile cichlid fish are less aggressive when reared with their parents (Taborsky & Oliveira, 2012), mother-deprived pullets fail to develop typical linear hierarchical order (Perré et al., 2002). Other studies show that social experience with adults (parents and non-parents) during development is crucial for the development of social behaviour and skills such as aggression regulation (elephants *Loxodonta Africana*: Slotow et al., 2000; campbell's monkeys *Cercopithecus campbelli campbelli*: Lemasson et al., 2005; horses, *Equus caballus* Bourjade et al., 2008; 2009), social cohesion (horses: Henry et al., 2012), learning and discrimination abilities (elephants: McComb et al., 2001), communication skills (birds and mammals: Snowdon & Hausberger, 1997; birdsong and humans: Goldstein et al., 2003; humans: Kuhl et al., 2003; canaries *serinus canaria*: Lehongre et al., 2006; European starlings: Poirier et al., 2004, Bertin et al., 2007; 2009; humans: Caskey et al., 2011) or multisensory representation of social familiarity (elephants: McComb et al. 2001; starlings: George et al., 2012). One of the foundations of social groups is the motivation of their members to aggregate, come together and interact with one another (Ward & Webster, 2016). Bees' social motivation is influenced by the early social environment (Hewlett et al., 2018). However, it is not yet clear whether

47 vertebrates' motivation for social behaviour is influenced by prior social experience (Templer
48 et al., 2018). The concept of prosociality has provided an additional framework for
49 developmental studies on social behaviour and skills (e.g. Kaplan 2020). The evolutionary roots
50 of prosociality as a "voluntary behaviour that benefits another" are still largely unknown,
51 especially as it has been mostly studied in primates (Marshall-Pescini et al. 2016), but evidence
52 or premises have also been found in birds (Kaplan 2020). Social motivation and the tendency
53 to have long lasting social bonds may be important underlying features (Cronin, 2012).
54 European starlings, like ravens, form lasting social bonds ("friendships") outside the breeding
55 season, that may also influence mating choices (Boucherie et al. 2018, Hausberger et al. 1995,
56 Henry et al. 2013; Teitelbaum et al 2017). In starlings, social bonds are reflected in shared
57 songs, i.e. social mimicry, also considered as a premise for prosociality. Kaplan (2020) suggests
58 that social bonding might precede the expressions of prosocial behaviour. She proposes that the
59 juvenile period is crucial in the development of such social skills, especially the phase when
60 juveniles, although independent for feeding, are still in close contact with their parents. Very
61 few studies have however been performed on these precise aspects and most studies on social
62 deprivation have used paradigms of social isolation that confound the need for social contact
63 (which may trigger an increased motivation for access to social stimuli) and the lack of certain
64 specific social influences which may decrease social motivation in a same species (e.g. horses:
65 Christensen et al. 2002; Bourjade et al. 2008).

66 At a time when there is a need for expanding animal models on the processes of the development
67 of social skills (Marshall-Pescini et al. 2016, Kaplan 2020), and to understand how altered
68 social skills impact social functioning (Contreras-Huerta, 2020), European starlings appear as
69 a particularly interesting species, given their propensity to develop lasting social bonds, song
70 sharing and intermodal social representations (e.g. Henry et al. 2013, George et al. 2011).
71 Moreover, wild-caught adult European starlings, are when isolated, highly motivated to trigger

sensors that enable them to see pictures of conspecifics (Perret et al., 2015), demonstrating the intrinsic rewarding value of social stimuli for social vertebrates (Borland et al., 2017). However, the absence of adults during starlings' development induces alterations of the auditory and multisensory representations of conspecifics (George et al., 2012; Cousillas et al., 2006; 2008) and of their reactions to a mirror image (Henry et al., 2008).

Here we hypothesized that the social motivation and representation of starlings raised without experience with adults would be altered. On one hand, we expected adult birds deprived of experience with adults to be less socially motivated, i.e. to "work" less for access to a social stimulus when in isolation than normal adults. On the other hand, since earlier studies showed alterations of social representations in such birds, we also expected them to show less differential motivation for social versus non-social stimuli than adults with a normal ontogeny. In order to answer these questions, we used, in hand-raised male starlings maintained in groups of same-age peers until adulthood without any contact with adults, a conditioning paradigm where access to visual stimuli was the reinforcer (described in Perret et al. 2015) 1) to test the motivation for social stimuli, and 2) the differences in motivation between social and non-social stimuli. By raising the birds in groups of peers, we avoided the confounding effect of social isolation to concentrate on the importance of adult presence *per se.* We compared these results to those obtained with birds wild-caught as adults (i.e. with a normal ontogeny), tested in the same conditions and at the same time (published in Perret et al. 2015): during the tests, the birds were placed in individual cages where they had to put their beak into a sensor to have visual access, on a computer screen placed inside the cage, to a picture of either unfamiliar conspecifics or landscapes.

METHODS

Ethics. All the experimental procedures were performed in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC) and approved by the departmental direction of veterinary services of Ille-et-Vilaine (licence number 35-238-15 and licence number 35-119).

Subjects

Eleven experimental (i.e. socially deprived) male starlings were this study's subjects which were tested at the same time as 10 "control" male birds wild-caught as adults. The experiments took place in April-May 2011, when the experimental birds were 2 years old (i.e. as adults). Therefore, both groups had spent at least 2 years in captive conditions. However, since the data on the control birds have been published earlier (Perret et al 2015), the comparisons are made here between the hand-raised birds and the published data.

The experimental birds were collected in nests (seven different broods, therefore one or two males per nest) in the wild when 1 week old (April 2009) in Rennes (France). They were hand-reared as a group with 8 female siblings and fed commercial pellets mixed with water for one month, until independence. They were then housed in an indoor aviary (2.1x1.05x2m), equipped with perches, where they were kept together with neither visual nor auditory contact with adult conspecifics. Once adult (2 years old), the eleven males were moved to individual test cages (60x39x65cm) placed in a soundproof chamber (sound attenuation of 35dB). Since isolation can stress starlings, we checked daily that they expressed typical behaviours using continuous video-recordings. Birds did not lose weight between the first and last day of the experiment. At the end of the study, after a maximum of 9 days in the experimental cages, the birds were returned to the indoor aviary and were kept for future studies. The control birds had

been captured in 2006, kept in an outdoor aviary in a large mixed group on Rennes University Campus and then placed in an indoor aviary 2 years before the beginning of the experiment.

Artificial light was adjusted weekly to the natural photoperiod. This light covered the solar spectrum from near-infrared to near-UV and was flicker-free (Osram T8 L18W/865 Lumilux cool daylight). Food (commercial pellets) and water were provided ad libitum. No food restriction of any kind was used throughout the whole study.

Visual Stimuli

Our methods were based upon Perret at al. (2005). Six colour pictures (1024 x 768 pixels) were used: 3 of three unknown adult male starlings and 3 of three different semi-urban landscapes (Figure 1a). To avoid possible biases due to sex preferences, the unknown starlings on pictures were individuals of the same sex as the test subject. The pictures were life-sized side views (on average 17 cm from beak to tail) of starlings with their yellow beak closed. These pictures were cut and pasted on a uniform neutral grey background (Gimp 2.6). The landscape pictures contained no animals, humans, cars or buildings. According to a 0:1 scale, the mean ratio of light: dark was 0.72 for the social stimuli (i.e. pictures of starlings) and 0.42 for the non-social stimuli (i.e. landscape pictures). The mean contrast was 0.25 for the social stimuli and 0.37 for the non-social stimuli. The order of presentation of the three pictures was randomized.

Apparatus (see Perret et al. 2015)

Each experimental cage (60x39x65cm) was equipped with a 15"LCD colour screen (NEC AccuSync LCD52VM) and was inside a sound-proof chamber to prevent external

142 interferences. The screen was attached to one end of the cage and protected by a transparent
143 acrylic glass pane (37.5x62.5cm). Two water dispensers and two food dispensers (providing
144 food and water ad libitum) were placed at the other end of the cage. Two perches were placed
145 parallel to the screen (at 15 and 35 cm from it respectively). The perch farthest from the screen
146 was equipped at each extremity with an optical sensor that enabled the birds to trigger the
147 stimuli. Starlings' bills are adapted to probing into the soil to find food. This feeding technique
148 is termed "prying" or "open-bill probing" (Feare, 1984). We took this natural behaviour into
149 account to develop an apparatus that starlings could use spontaneously. When starlings put their
150 beak in a hole it cut an infrared beam between an IR emitter and an IR detector and thus
151 triggered the display of a visual stimulus on the screen for nine seconds (see Protocol below).
152 The sensors were connected to a computer (Dell Inspiron Mini 10 PP19S or Asus Eee PC
153 T91MT) that controlled the display of stimuli and recorded every beak insertion into the
154 sensors. When a starling inserted its beak into a sensor either during the 9-second display of a
155 stimulus or during a refractory period of one second after the display, no other display was
156 triggered. However, this beak insertion was recorded. When starlings were not being tested they
157 did not have access to the sensors (Figure 1a). None of the starlings had ever experienced this
158 apparatus previously.

159

160 **Experimental procedure (see Perret et al. 2015)**

161 After a 2-day habituation period in the experimental cage to avoid biases due to novelty,
162 birds were subjected to two 30-minute familiarization sessions (one in the morning from 10:15
163 am to 10:45 am; one in the early afternoon from 2:20 pm to 2:50 pm; GMT+2) with the visual
164 stimuli that would be used during the experiment. The birds did not have access to the sensors
165 during this familiarization phase. During each session, each of the six pictures was displayed

166 on the screen for 9 seconds and appeared only once. Time intervals between two pictures (while
167 the screen displayed a neutral grey background) varied randomly from 2 to 6 minutes (five-time
168 intervals: 2, 3, 4, 5 and 6 minutes). At the end of this familiarisation phase, each bird had seen
169 each stimulus twice.

170 The day following the familiarization sessions, starlings were given access to the sensors
171 seven hours a day, from 11:00 am to 06:00 pm (local time: GMT +2). Recordings began as soon
172 as a starling triggered the display of a stimulus spontaneously by inserting its beak into an
173 optical sensor. One starling had not triggered any stimulus after two days in the test cage. The
174 sensors of this starling were then baited with a small quantity of highly appetizing extra food
175 (insectivorous universal preparation), which came in addition to the commercial pellets. This
176 was sufficient to induce this starling to start using the sensors and to keep using them without
177 bait. The subjects were kept in their test cage for six consecutive days starting from the day
178 they first triggered the stimulus display. This test period is within the range of durations used
179 in other operant conditioning studies of birds (2-40 days) (Adret, 1993; Collins; 1999; Okanoya
180 et al., 2000; Appeltants et al., 2005). The six days were divided into 2x2 days of stimulation
181 and 2 days with no stimulation. During the first two days of the stimulation phase, one sensor
182 triggered the display of a landscape picture and the other the display of a picture of a conspecific
183 (configuration 1), and the association sensor/picture-type was then reversed (configuration 2)
184 for the next two days (Figure 1b). We used these two configurations to avoid biases due to a
185 preference for one side (right or left). The first configuration was determined randomly and
186 counterbalanced across subjects. When the display of a stimulus was triggered the picture was
187 displayed for nine seconds and another second was necessary before a new stimulus could be
188 displayed (refractory period). When no stimulus was displayed, the screen displayed a uniform
189 grey, the same as the grey background of the stimuli. The stimulation phase was followed by
190 two days without stimulation. During these two days, starlings still had access to the sensors

for seven hours a day but the sensors no longer triggered a display of a stimulus and the screen displayed continuously the same uniform grey picture as during the stimulation phase. The computer kept recording every beak insertion into the sensors during this phase.

Data collection and analysis

The daily numbers of beak insertions (including the total number of beak insertions during the display of a stimulus and during the refractory period; see above) were used to compare the stimulation and non-stimulation phases. The numbers of effective triggers (that is excluding beak insertions during the display of a stimulus on the screen or during the refractory period) were used to compare: 1) the four days of stimulation with both stimuli, and 2) the two types of stimuli (pictures of conspecifics / landscape pictures).

Non-parametric statistical analyses were used on individual absolute values, with an acceptation level of $p<0.05$ (Statistica 10 for Windows, StatSoft Inc.). Friedman analyses of variance by ranks were used to compare the four days of stimulation across subjects. Wilcoxon signed-rank tests were used to compare the data of the stimulation and non-stimulation phases and the data for the two types of stimuli (pictures of conspecifics / landscape pictures) across subjects. Chi-square (χ^2) tests were used to compare data for the two types of stimuli (pictures of conspecifics / landscape pictures) for each subject. All statistical tests were two-tailed and unless otherwise indicated, data are presented as mean ± standard error of the mean (SEM) and median when appropriate.

Data on birds wild-caught as adults had already been published (Perret et al. 2015), but we conducted nevertheless direct statistical comparisons between both groups of birds.

RESULTS

Six of the eleven hand-raised starlings involved in the experiment inserted their beak into the sensors spontaneously, on average 180 ± 71 times during the four days. Five starlings did not complete the four days of stimulation and stopped using the sensors or used only one sensor, either the left or the right one. Four of these starlings made a choice on at least one day: two preferred the image of a conspecific and two preferred the landscape image. However, to improve accuracy, we kept only the data of the six motivated individuals for further analyses. Despite their high motivation, their rate of beak insertions was only half that of wild-caught starlings in the same experimental situation (367 ± 105 *versus* 180 ± 71, although this difference did not reach statistical significance, due to high individual differences in both groups (Mann-Whitney, U=13, N1wca=7, N2hr=6, p=0.11) (see Perret et al., 2015). Individual variability was high: for example, one starling (B3) inserted its beak into the sensors 48 times during the four days (X=12 ±7.6 per day) whereas another one (B2) inserted its beak into the sensors up to 235 times during a single day (with an average of 129.25 ± 101.4 per day). These beak insertions nevertheless indicated a real motivation to see pictures because they were significantly less frequent during the non-stimulation phase (13 ± 4 times per day, median: 13,0) than during the stimulation phase (95 ± 35 times per day, median: 60,5) (Wilcoxon test: z=2.201, N=6, p=0.03) (Figure 2a). This showed that the subjects found the visual stimuli rewarding. Moreover, the numbers of triggers did not change significantly across the four-day period, whatever the stimulus, which showed that there was no loss of interest with time (Friedman analysis of variance: χ^2=1.8, df=3, N=6, p=0.61). Fifty-five percent of all the starlings therefore appeared to be genuinely motivated by and interested in the pictures.

During the stimulation phase, four of the six starlings expressed an active choice between the two types of stimuli (Figure 2b). However, this choice varied from one starling to another. Two of the six starlings triggered the landscape pictures significantly more often than the pictures of conspecifics (B1: χ^2=35.35, ddl=1, p<0.001; B5: χ^2=25.63, ddl=1, p<0.001) whereas two other starlings triggered the pictures of conspecifics significantly more often than the landscape pictures (B4: χ^2=115.5, ddl=1, p<0.001; B6: χ^2=21.6, ddl=1, p<0.001). The other two starlings showed no preference for one type of stimulus (B2: χ^2=2.65, ddl=1, p=0.1; B3: χ^2=0.08, ddl=1, p=0.77). As a group, hand-reared male starlings thus triggered the pictures of conspecifics as frequently as they triggered the landscape pictures (97 ± 42 times for the pictures of conspecifics; 83 ± 36 times for the pictures of landscapes) (Wilcoxon test: z=0.105, N=6, p=0.92) (Figure 2b). Moreover, these hand-reared triggered statistically less a picture of a conspecific than birds wild-caught as adults, tested with the exact same experimental design (Mann-Whitney, U=9, N1=7, N2=6, p=0.05) whereas no difference could be evidenced when considering landscape picture (Mann-Whitney, U=15, N1=7, N2=6, p=0.18). These results indicated that a picture of a conspecific did not have the same value for both groups of birds.

DISCUSSION

Although raised in a social environment with peers, male isolated adult starlings that had been deprived of social experience with adults during their development appeared to be less motivated to "work" to see a picture of a conspecific than starlings wild-caught as adults who had had a normal ontogeny. They triggered starling pictures half as frequently as birds wild-caught as adults (see Perret et al. 2015). In addition, they did not show, at the group level, a greater motivation to see conspecific compared to landscape pictures. Moreover, only half of the experimental birds showed a consistent motivation to trigger the display of a picture, whereas all birds wild-caught as adults had previously proved to be motivated (Perret et al., 2015). Thus, while birds that developed in the wild seemed to have a natural yearning for social

stimulation, starlings raised without any contact with adults appeared to either consider pictures as mere "visual enrichments", regardless of their content, or they did not bother to work to see them. Pictures of conspecifics did not appear here as a social reward. Therefore, the absence of experience with adults during development appears to lead to altered social motivation and representation.

There are some limitations to the study: 1) the hand-reared birds were somewhat younger (although adult) than the control birds, although there is no evidence, to our knowledge, that social motivation increases with age in adults, 2) the ideal control group would have consisted in birds bred in captivity and raised by parents, so as to have the same captive environment as the experimental birds all along. However, European starlings are very difficult to breed in captivity (the young often die in the nest) and therefore this option would have been too hazardous. At least, birds caught as adults have had experience with their parents during development which was the main point.

Beyond these limitations, our results converge with other studies showing that experience with adults during development is necessary to develop appropriate social cognition and that the absence of social contact with adults affects social abilities (Hesse & Thünken, 2014; Arnold & Taborsky, 2010). It was already known that the presence of adults during development is important for social functioning such as the regulation of aggression and appropriate dominance hierarchy structuring (Slotow et al., 2000; Bourjade et al., 2008, 2009, Perré et al. 2002). A recent study on a crab species (*Neohelice granulata*) demonstrated that social isolation has a negative effect on long term memory retention of both aversive or appetitive tasks (Santos et al, 2021). However, here we show that even the social motivation for conspecific cues can be affected, although the birds had been raised in a group and were isolated at the time of testing. This finding confirms the importance of the early social environment, from bees (Hewlett et al., 2018), to vertebrates (Templer et al., 2018), including

288 birds (Kaplan 2020; Teitelbaum et al, 2017), for developing social motivation. Social
289 motivation is a prerequisite for the evolution of prosociality, and its first steps such as social
290 bonding. Kaplan (2020) proposed that the juvenile stages, and especially those when the young
291 are still in contact with parents, are especially crucial for developing social attachment. The
292 present results add to earlier findings in starlings showing that adult-deprivation during
293 development induce deficits in brain processing of social information (Cousillas et al. 2004,
294 2006, George et al. 2010, 2012) and to the still too limited literature in birds (Marshall-Pescini
295 et al; 2016). Starlings' motivation to see pictures of other starlings is a promising tool for
296 studying the social rewards that knit communities together (Weiler, 2015), further
297 investigations could include testing further the possible premises of prosociality in this
298 promising species.

299 Social bonding, an important feature of starlings' social life, is also based on social
300 representation. Young horses and starlings raised without adults do not show the clear bonding
301 shown by normal adults and present a rather loose social organization (Bourjade et al. 2008),
302 which also affects starlings' song sharing pattern (Bertin et al. 2007). Interactions with adults,
303 by promoting selective attention (Kuhl et al., 2003; Bertin et al., 2007, 2009; Chen et al., 2016),
304 could help refine adult characteristics through perceptual tuning (Olmstead & Kuhlmeier, 2015)
305 and help orienting responses towards appropriate partners (Kaplan 2020). Our results clearly
306 indicate that the capacity of considering conspecifics as suitable partners depends on early
307 social experience. This experimental design will allow however to test if the social valence of
308 an individual in the picture modifies the birds' reaction (Cronin, 2012) and also to test for
309 possible hormonal mechanisms of complex social behaviour (Duque et al, 2018, 2020).

310

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316

317 **Ethical statement**. The experiments were performed in France (licence number 35-238-15 and
318 licence number 35-119 issued by the departmental direction of veterinary services of Ille-et-
319 Vilaine). The licences issued by local veterinary services do not specify that the birds should
320 be released. They certify that our captive starlings are regularly checked to make sure that they
321 are disease free and that the experiments are performed in accordance with the European
322 Communities Council Directive of 24 November 1986 (86/609/EEC).

323

324 **Data accessibility**: Data are available from the Figshare repository:
325 https://doi.org/10.6084/m9.figshare.12453695.v1

326 **Authors' contribution**. LH, HC, MH and IG conceived, designed and supervised the
327 experiments. AP and MC designed and performed the experiments. AP analysed the data. AP,
328 LH, MH and IG wrote the paper.

329 **Competing interest**. The authors declare no competing interests.

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335

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503 **Figure captions**

504 **Figure 1.** Experimental apparatus and protocol. (a) Picture displays are triggered by beak
505 insertions into optical sensors controlled by a computer (see text for more details). Inset on the
506 left shows a magnified view of one sensor and illustrates how a starling can trigger the visual
507 stimuli by inserting its beak into the sensor. Inset in the top right-hand corner shows the two
508 types of pictures that were used as visual stimuli with, from top to bottom, social stimuli
509 (pictures of unknown male starlings) and non-social stimuli (landscape pictures). Although the
510 pictures are presented here in black and white, they were displayed in colour during the
511 experiments. The uniform grey background of the starlings' pictures was the same as the
512 uniform grey that was displayed continuously between triggers and during the non-stimulation
513 phase (see Perret et al. 2015). (b) Protocol: Configuration 1 (2 days): either landscape pictures
514 were triggered by the left sensor and pictures of conspecifics were triggered by the right sensor
515 or the reverse; Configuration 2 (2 days): the previous configuration was reversed.

516 **Figure 2.** (a) Daily numbers of beak insertions into the sensors during the stimulation and non-
517 stimulation phases. (b) Numbers of triggers of pictures of conspecifics and landscape pictures.
518 Open symbols connected by lines: individual values. Open circles with error bars: mean +/-
519 SEM obtained across starlings. *: $p<0.05$ (Wilcoxon test on individual values). B: bird.

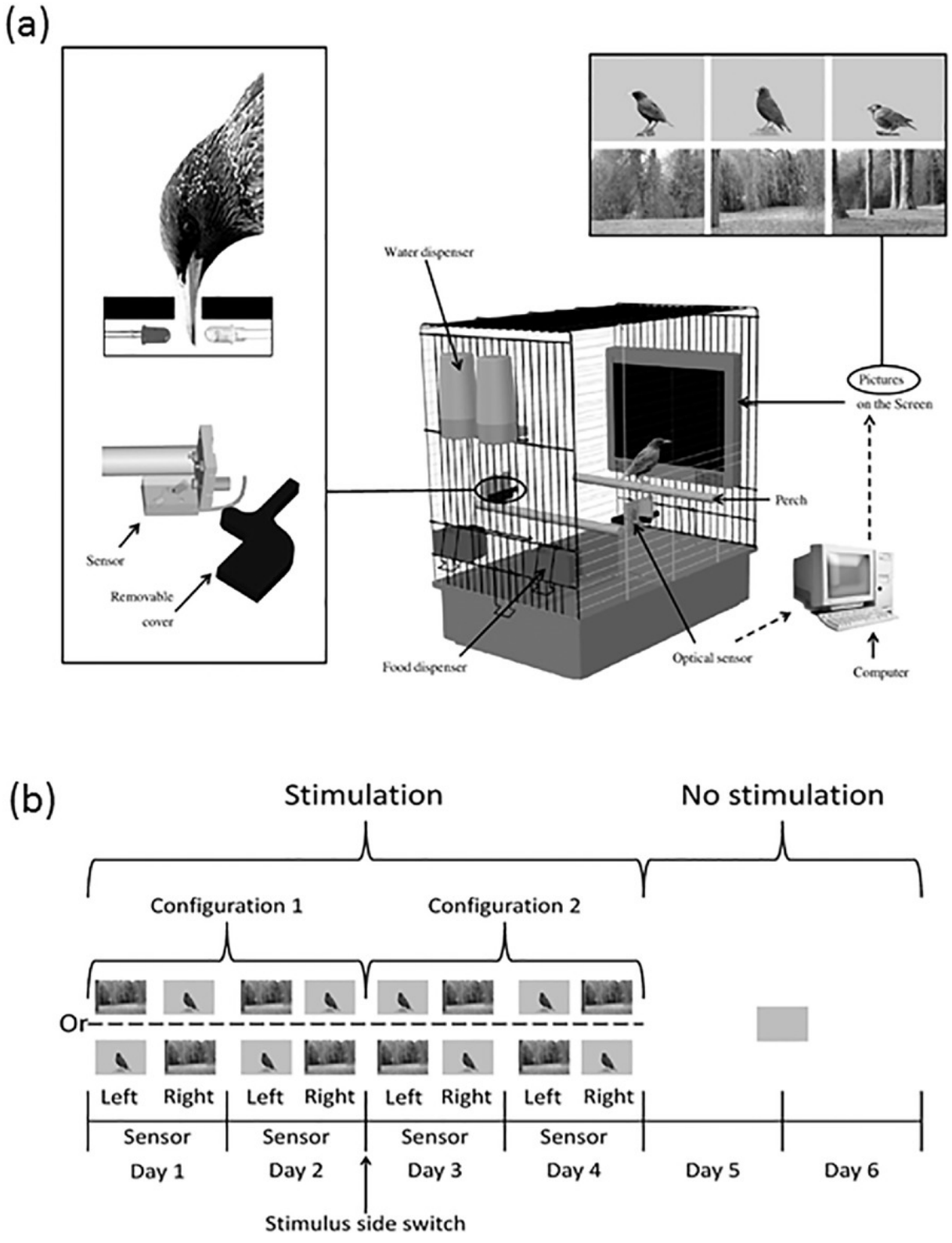

FIGURE 1

Experimental apparatus and protocol. (a) Picture displays are triggered by beak insertions into optical sensors controlled by a computer (see text for more details). Inset on the left shows a magnified view of one sensor and illustrates how a starling can trigger the visual stimuli by inserting its beak into the sensor. Inset in the top right-hand corner shows the two types of pictures that were used as visual

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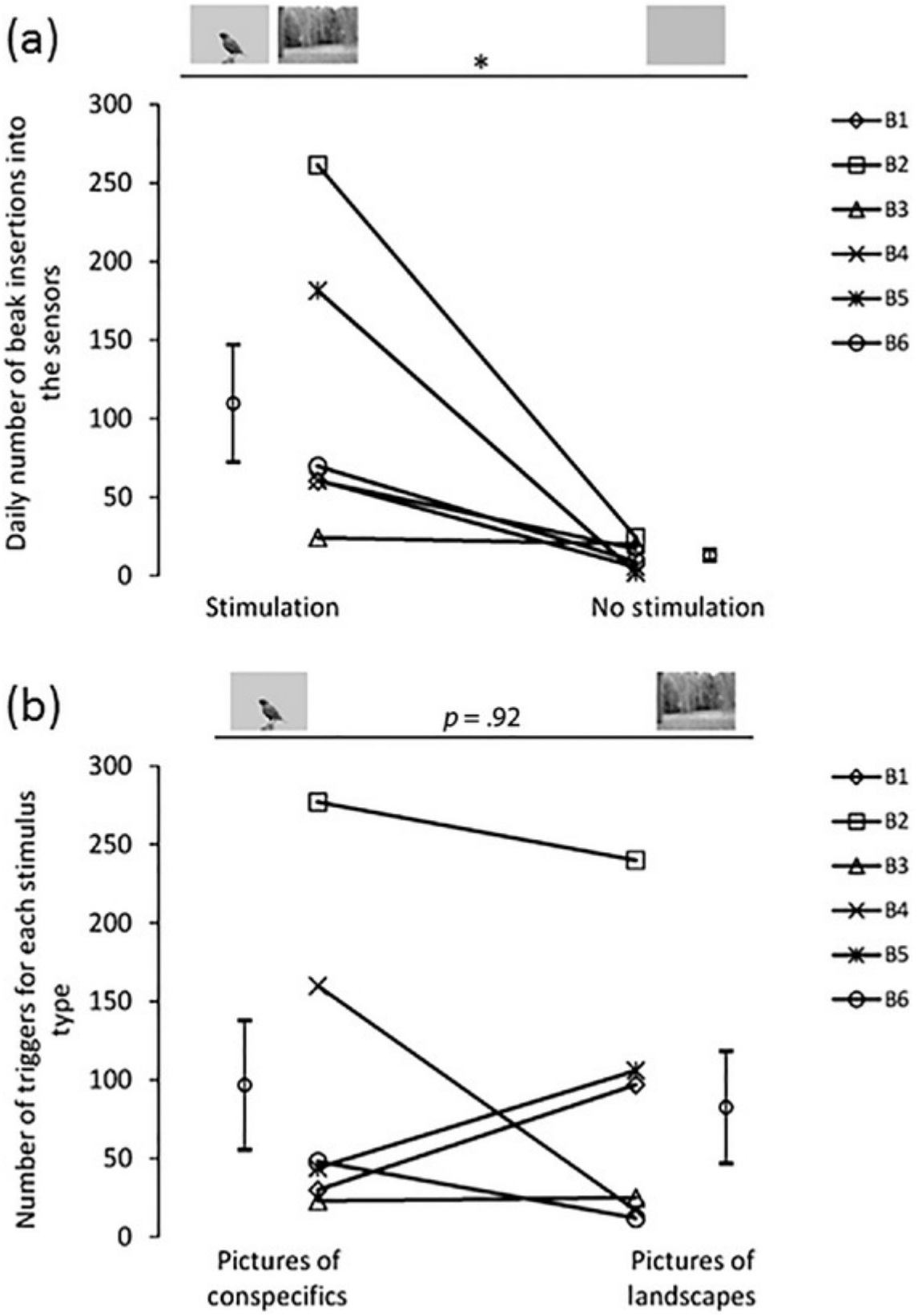

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