
*Original article*Giorgio Vallortigara · Lucia Regolin
Margherita Rigoni · Mario Zanforlin**Delayed search for a concealed imprinted object in the domestic chick**

Received: 17 January 1998 / Accepted after revision: 29 March 1998

Abstract Five-day-old chicks were accustomed to follow an imprinted object (a small red ball with which they had been reared) that was moving slowly in a large arena, until it disappeared behind an opaque screen. In experiments, each chick was initially confined in a transparent cage, from where it could see and track the ball while it moved towards, and then beyond, one of two screens. The screens could be either identical or differ in colour and pattern. Either immediately after the disappearance of the ball, or with a certain delay, the chick was released and allowed to search for its imprinted object behind either screen. The results showed that chicks took into account the directional cue provided by the ball movement and its concealment, up to a delay period of about 180 s, independently of the perceptual characteristics of the two screens. If an opaque partition was positioned in front of the transparent cage immediately after the ball had disappeared, so that, throughout the delay, neither the goal-object nor the two screens were visible, chicks were still capable of remembering and choosing the correct screen, though over a much shorter period of about 60 s. The results suggest that, at least in this precocial bird species, very young chicks can maintain some form of representation of the location where a social partner was last seen, and are also capable of continuously updating this representation so as to take into account successive displacements of the goal-object.

Key words Delayed response · Imprinting · Memory · Chick · *Gallus gallus*

Introduction

In spite of a folk reputation of not being a very clever animal, the domestic fowl has proved to possess remarkable cognitive abilities (reviews in Rogers 1995, 1997). On their second day of life, domestic chicks appear able to recognize partly occluded objects (Regolin and Vallortigara 1995; Lea et al. 1996; see also Forkman 1998), an ability that in human infants appears only at around 6–7 months (Kellman and Spelke 1983). Chickens can learn to discriminate between images of conspecifics and allospecifics as categories, and seem to be better at discriminating images of individual conspecifics than pigeons (Ryan 1982; Ryan and Lea 1994). Young chickens can form spatial representations using both nearby and distant landmarks (Rashid and Andrew 1989), as well as the geometrical arrangement of surfaces as surfaces in the environment (Vallortigara et al. 1990; Tommasi et al. 1997). Using devaluation techniques, it has been shown that hens possess declarative representations (Forkman 1997). Ethological studies have also delineated sophisticated abilities associated with the social life of this species. For instance, it has been shown that in the maternal display that attracts the chicks to feed on suitable nutritious items, broody domestic hens appear to be sensitive to feeding errors made by their chicks (Nicol and Pope 1996). Also, it has been claimed that food calls and alarm calls of domestic chickens are “functionally referential”, including information about the eliciting stimulus (Evans et al. 1983), and that they are produced with “intent to inform” – and sometimes even “to misinform” (see Marler et al. 1986 a, b).

In a recent series of studies, we have investigated the solution of detour problems by young chicks. Contrary to previous claims (e.g. Koehler 1925; but see Scholes 1965; Scholes and Wheaton 1966; Etienne 1973, 1984), we found that, providing certain perceptual and motivational factors were taken into account, chicks as young as 2 days successfully mastered detour problems (Regolin et al. 1994, 1995a,b). Most interestingly, using an artificial imprinted object as goal, we found that chicks searched for

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and eventually reached it successfully, even in the absence of any local acoustic, olfactory or visual orienting cues (Regolin et al. 1995a). This result suggests that chicks could maintain some sort of representation of the location (and thus of the presence) of a social partner even when it was no longer available to direct perception.

This ability to form an internal representation of a “disappeared” object nevertheless has important limitations. For instance, although it has been confirmed that chicks do have an “object concept” that maintains a representation of the object in the absence of direct sensory cues, it appears that they are unable to predict the resting position of a moving imprinted ball from its direction of movement prior to occlusion (Freire and Nicol 1997; but see also Krushinskii 1970; Haskell and Forkman 1997, for further studies on adult animals using food incentives). Nonetheless, whatever chicks are able to represent and remember, it is interesting to investigate the temporal characteristics of this behavioural capacity: how long can a young chick remember the spatial location of an imprinted object that has disappeared behind an occluding object?

These sorts of issues have been investigated since early in this century, mainly in mammals, using the so-called “delayed response problem”, developed by Hunter (1913). In a typical test, the subject watches the experimenter while the latter places a preferred food incentive under one of two identical, or different, objects. During a subsequent delay period the animal has no physical access to the objects (in some studies they have visual access to the objects, whereas in others the objects are hidden from view). After the delay period the animal is allowed to choose between the two objects; obtaining the food more frequently than expected by chance is assumed to indicate that the animal remembers where it was placed initially and chooses on the basis of that information (Wu et al. 1986). When food is used as the incentive, even primates (e.g. macaques) perform at chance levels after delays longer than 30–40 s (Fletcher 1965; Rumbaugh and Gill 1975). Similar results have been reported for several other species of mammals, although results varied considerably depending on procedural variables (Tinklepaugh 1928; Fletcher 1965). When social stimuli were used as the incentive, infant pigtailed macaque monkeys reliably chose the correct stimulus with delays up to 60 s (Wu et al. 1986).

Very little is known about delayed responses in avian species. Object permanence has been studied in birds, but without investigating the delayed response problem (Pepperberg and Kozak 1986; Pepperberg and Funk 1990; Dumas and Wilkie 1995; Funk 1996). The so-called matching-to-sample task is obviously derived from the delayed response problem and has been widely used in studies of the pigeon and other avian species, but, typically, the delays used are very short (of the order of seconds or milliseconds). When a 1.5-s delay is used, domestic hens seem to perform as well as pigeons in delayed matching-to-sample tasks (Foster et al. 1995). However, no data are available for longer delay periods. On the other hand, it is

doubtful that delayed matching-to-sample tasks using conditioning procedures would be performed very efficiently by young chicks. We thus chose to adapt a natural and highly adaptive response of young chickens (i.e. looking for a “disappeared” imprinted object) to investigate the delayed response problem.

Experiment 1

Subjects

The subjects were 52 (27 males and 25 females) Hybro chicks obtained from a commercial hatchery (Incubatoio Alba, Ponte di Castegnero, Vicenza) when they were only a few hours old. They were reared singly, at a controlled temperature (30–35 °C), with food and water available ad libitum. The rearing cages (45 cm wide × 25 cm high × 35 cm deep) were illuminated from above by fluorescent lamps. A small red plastic ball (4 × 3 × 3 cm) was suspended by a fine thread (at about head height for the chick) in the centre of each rearing cage and served as the imprinting object (previous studies have shown that this stimulus is very effective in producing social attachment in the chick; Vallortigara and Andrew 1991).

Apparatus

The test apparatus (shown in Fig. 1) consisted of a wide circular arena (95 cm diameter). The arena was made of aluminium, its outer wall was 30 cm high, and the floor was uniformly covered by sawdust (1 cm thick). The only light in the experimental room was a 40-W lamp situated

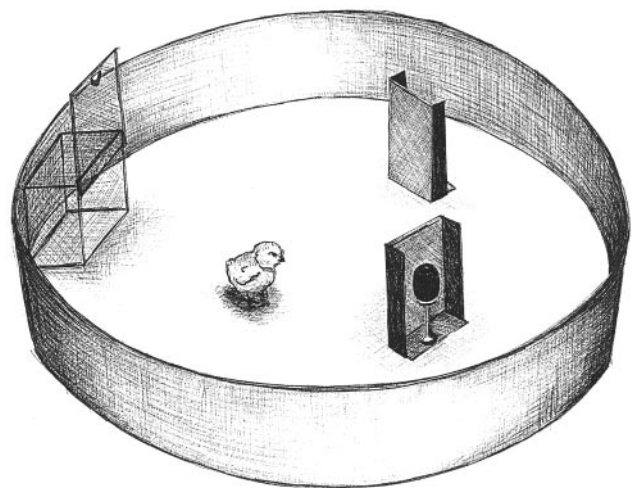


Fig. 1 Schematic representation of the apparatus used to test the duration of a chick's memory for the location of an object that has disappeared. While the chick was confined in the *transparent enclosure*, the imprinting object was made to disappear behind either one of two opaque *screens*. The chick was then allowed to approach the screens either immediately after disappearance of the imprinted object, or after a certain delay

just above the centre of the arena itself. Within the arena, adjacent to the outer wall, was positioned a small clear-glass cage (10 × 20 × 20 cm), where the chick could be confined for the required delay period during the test phase. The side of the glass cage facing the centre of the arena was removable (the experimenter could lift it from above) to release the test chick in the arena (see Fig. 1). Two opaque screens (made of yellow cardboard, 16 × 8 cm, with 3-cm sides bent back to prevent chicks from spotting the hidden ball) were positioned symmetrically with respect to the glass cage in the centre of the arena, 20 cm apart from each other and 31 cm from the closest side of the glass cage.

Procedure

On day 5, each chick underwent preliminary training. For the training, only one of the two yellow screens was used, and positioned in front of and 31 cm away from the glass cage. The chick, together with the imprinting red ball, was at first placed within the arena, free to move around for a couple of minutes and get acquainted with the novel environment. The rearing ball, held from above (on a fine thread) by the experimenter (not visible to the chick), was slowly moved and made to disappear behind the screen. This was repeated a few times, until the chick promptly responded by following, and finding, the ball behind the screen. Thereafter, the test chick was confined in the glass cage. The red ball, outside the cage, was slowly moved until it disappeared behind the yellow screen; the experimenter took care that the chick saw this happening. The chick was then immediately set free in the arena, and every time the chick rejoined the ball behind the screen it was allowed to spend a few seconds next to its artificial companion. Training ended when the chick reached the ball behind the screen within 10 s of release three times consecutively.

Testing took place about 2 h after training. Two identical yellow screens were positioned in the arena as shown in Fig. 1. The chick was confined in the transparent glass-cage, from where it could see and track the ball disappearing behind one of the two screens. (The ball was moved down to the centre between the screens and then to the right or left.) After a certain delay, the chick was set free and could look for the ball behind either screen. The screen chosen first and searched by the chick was considered to be the response. A choice for the screen behind which the ball had disappeared was considered to be correct, a choice of the other screen was considered to be incorrect. If no screen was searched within 1 min of release, the trial was considered invalid. To check for consistency in the experimenter's judgements, video recordings of chicks' choices were also showed to "blind" observers (i.e. they did not know the position of the ball): agreement between experimenters and blind observers was 100%. Each chick performed 16 trials, and the screen behind which the ball disappeared was changed according to a semi-random sequence (Fellows 1967). The delay period between

the disappearance of the goal and the release of the chick was different for separate groups of chicks. The delay periods considered (and the number of chicks in each condition) were respectively: 0 s (4 males and 4 females); 30 s (5 males and 5 females); 60 s (5 males and 4 females); 180 s (6 males and 5 females) and 240 s (7 males and 7 females).

Percentages of correct responses with the various delay periods were analysed by analysis of variance (ANOVA), and significant departures from the chance level (50%) were estimated by one-sample two-tailed *t*-tests on the independent samples. Percentages of invalid responses were also analysed by ANOVA.

Results

Percentages of choices for the correct screen are shown in Fig. 2. The ANOVA revealed a significant main effect of the delay period [$F(4,42) = 4.891$; $P = 0.0025$]. There were no other statistically significant effects [sex: $F(1,42) = 0.180$; sex × delay ($F(4,42) = 0.572$)]. A preference for the correct screen occurred up to a delay period of 180 s; at greater delays choice became random (see Fig. 2).

Trials of those chicks that did not exit the glass cage, or that did not approach any screen, within 1 min (i.e. the invalid trials) were excluded from this analysis. Data from the invalid trials are shown in Fig. 3.

An analysis of variance performed on the data from the invalid trials revealed only a non-significant trend for a sex × delay interaction [$F(4,42) = 2.100$; $P = 0.0979$]. There were no other statistically significant effects. Results, thus, suggested a tendency for an increase in invalid

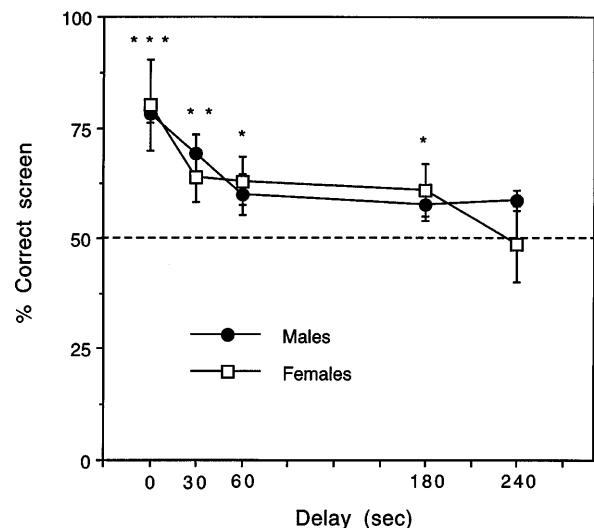


Fig. 2 Mean percentages (\pm SEM) of choices for the correct screen (the one behind which the imprinted object had disappeared) in experiment 1 as a function of the delay period between disappearance of the object and releasing of the chick from the transparent enclosure. Significant departures from chance level (50%) are indicated by the asterisks (* $P < 0.02$, ** $P < 0.01$, *** $P < 0.001$; two-tailed one-sample *t*-tests)

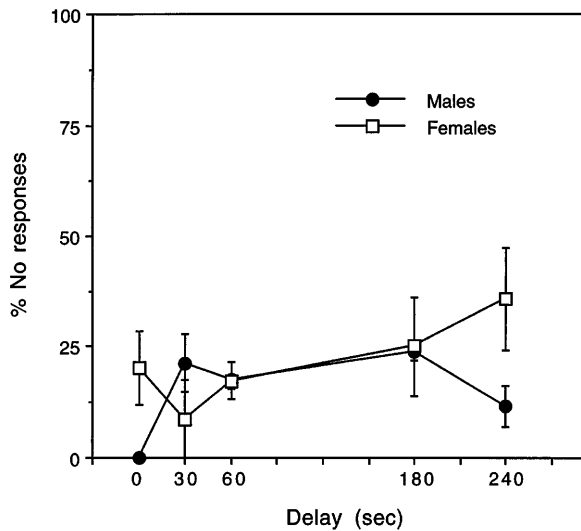


Fig. 3 Mean percentages (\pm SEM) of invalid responses in experiment 1 as a function of the delay period between disappearance of the object and chick's release

trials with increasing delay particularly in females, but the effect did not reach statistical significance.

Experiment 2

In experiment 1 the imprinting object disappeared behind one of two identical screens, symmetrically positioned with respect to the chick's starting point. The only cue available for the chick to orient towards the correct screen was thus given by its position in space, i.e. left or right. To check whether the presence of additional cues could affect, i.e. improve, chicks' performance, the two screens were made very different in colour and pattern and, as a result, two cues (the visual characteristics and position of the screens) were now available for the chick to use to distinguish between the correct and the incorrect screen.

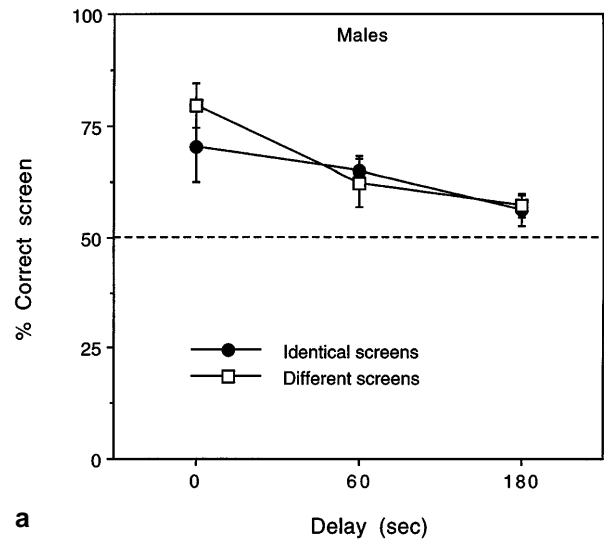
Subjects

A total of 60 chicks (30 males and 30 females) were used. Rearing conditions were exactly the same as described for experiment 1.

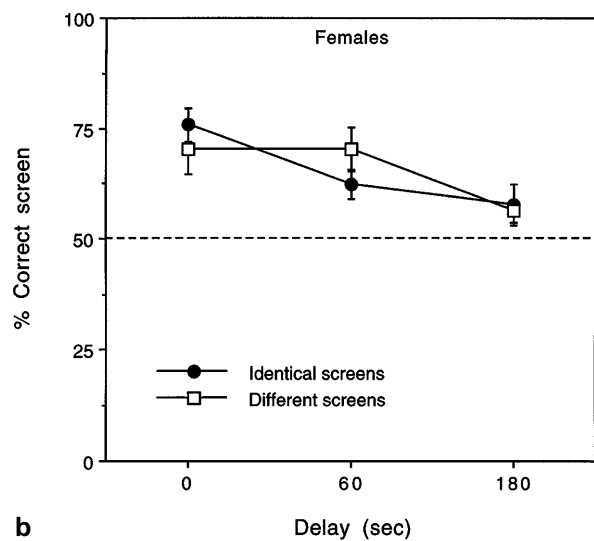
Apparatus and procedure

The apparatus was identical to that described in experiment 1. The two screens were now visually different in colour and pattern: one was blue with a yellow "X", the other white with a red "Florence lily" pattern.

The procedure was similar to that described in experiment 1. During training both screens were used alternately for each chick. In the experiment, the two screens maintained a fixed position in space for each chick: half



a



b

Fig. 4a, b Mean percentages (\pm SEM) of choices for the correct screen in experiment 2, using identical or different screens, in **a** male and **b** female chicks, as a function of the delay period between disappearance of the object and chick's release

of chicks had the blue-yellow screen on their right side, and the other half had the white-red one on their right side throughout the test phase. All other details of the procedure were identical to those described for experiment 1. Delay periods considered were: 0, 60, and 180 s; for each condition 12 chicks (6 males and 6 females) were used. A control group of 24 chicks was trained and tested with the same schedule as in experiment 1; delay periods considered for the control group were also of 0, 60 and 180 s, with 8 chicks (4 males and 4 females) tested in each condition, respectively.

Results

Percentages of choices for the correct screen are shown in Fig. 4. The ANOVA with sex, delay, and type of screen

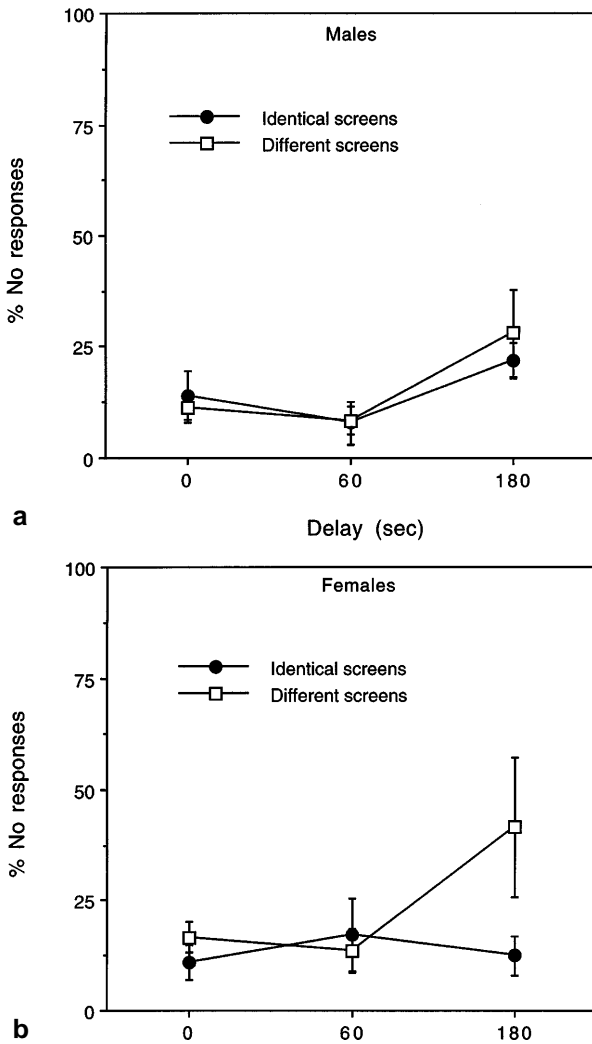


Fig. 5 a, b Mean percentages (\pm SEM) of invalid responses in experiment 2 using identical or different screens in **a** male and **b** female chicks as a function of the delay period between disappearance of the object and chick's release

(identical or different screens) as between-subjects factors revealed a significant main effect of the delay [$F(2,48) = 12.742$; $P = 0.0001$]. There were no other statistically significant effects [sex: $F(1,48) = 0.016$; type of screen: $F(1,48) = 0.240$; sex \times delay: $F(2,48) = 0.235$; sex \times type of screen: $F(1,48) = 0.152$; delay \times type of screen: $F(2,48) = 0.096$; sex \times delay \times type of screen: $F(2,48) = 1.690$]. Chicks chose the correct screen in all of the three conditions of delay, and this occurred both with identical [0 s: $t(7) = 5.576$, $P = 0.001$; 60 s: $t(7) = 6.057$, $P < 0.001$; 180 s: $t(7) = 2.533$, $P = 0.0379$] and with different [0 s: $t(11) = 6.469$, $P < 0.001$; 60 s: $t(11) = 4.373$, $P = 0.001$; 180 s: $t(11) = 3.995$, $P = 0.002$] screens.

Percentages of invalid trials are shown in Fig. 5. An ANOVA on these data revealed a significant effect of delay [$F(2,48) = 4.06$; $P = 0.0235$], mainly due to the increase in invalid responses with the longest time interval (180 s). There were no other significant effects [sex: $F(1,48) = 0.594$; type of screen: $F(1,48) = 1.716$; sex \times

delay: $F(2,48) = 0.183$; sex \times type of screen: $F(1,48) = 1.008$; delay \times type of screen: $F(2,48) = 1.761$; sex \times delay \times type of screen ($F(2,48) = 0.755$].

Experiment 3

In both experiments 1 and 2, once the imprinting object had disappeared, the test chick could keep visual contact with the environment through the transparent walls of the glass cage. Although it was clear that chicks did not spend all of the time with their bodies oriented towards the correct screen (they actually moved continuously within the glass cage, attempting to leave it), the fact that the screens were visible throughout the delay period could have affected the chicks' performance. In the next experiment, an opaque partition was used to prevent the test chick from seeing the two screens during its confinement in the glass cage. To check for any possible disturbing effect due to the positioning of the novel opaque screen in front of the glass cage, either chicks were accustomed during the training phase to the presence of the opaque screen, or they experienced the opaque partition for the first time during the test.

Subjects

A total of 64 (32 male and 32 female) chicks were used. Rearing conditions were the same as in previous experiments.

Apparatus

The apparatus was the same as in previous experiments. This time, however, an opaque partition (20 \times 20 cm) made of brown cardboard was used as an occluder, and positioned in front of the transparent glass cage during the delay between ball disappearance and release of the test chick.

Procedure

There were two groups of chicks. For the first group ("not habituated": 18 males, 18 females), the training procedure was the same as in the previous experiments. During the testing, however, the cardboard partition was positioned by the experimenter in front of the glass cage immediately after the red ball disappeared behind one of the screens. At the end of the delay period, the opaque partition was removed together with the removable side of the glass cage, releasing the test chick in the arena. In the second group ("habituated": 14 males, 14 females) the opaque partition was used in the same way as during initial training (with the single, central, screen) so that chicks were already accustomed to the presence of the partition before testing.

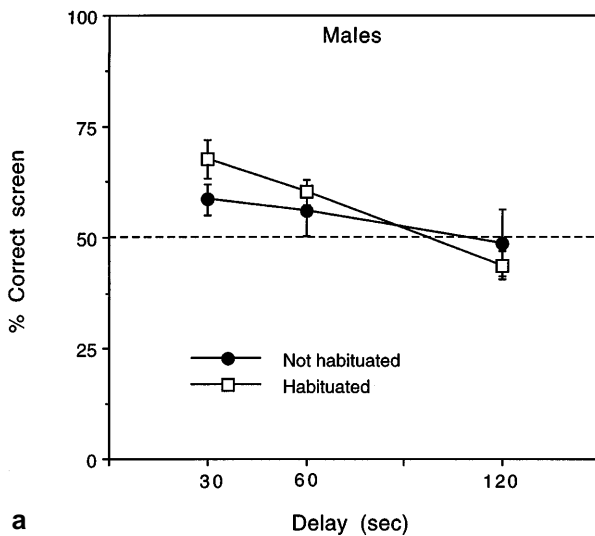
The delays tested (and number of chicks in each condition) were respectively: 30 s (not habituated: 6 males and 6 females; habituated: 5 males and 5 females), 60 s (not habituated: 6 males and 6 females; habituated: 4 males and 4 females), and 120 s (not habituated: 6 males and 6 females; habituated: 5 males and 5 females).

Results

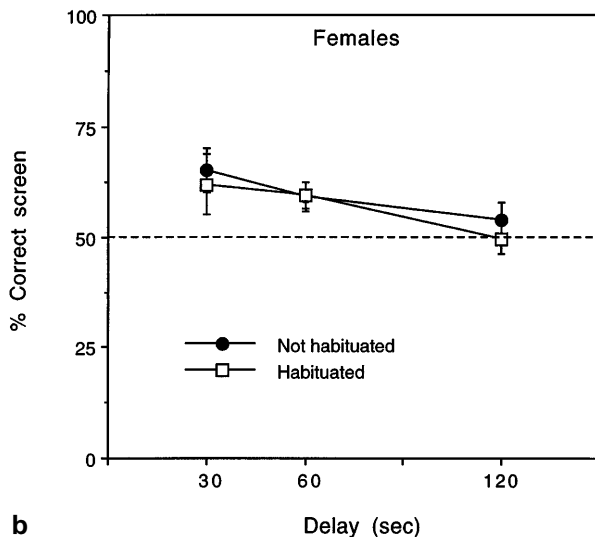
Chicks' choices are shown in Fig. 6. The ANOVA revealed a significant main effect of the delay period [$F(2,52) = 9.088$; $P = 0.0004$]. There were no other statistically significant effects [sex: $F(1,52) = 0.79$; habitua-

tion: $F(1,52) = 0.006$; sex \times delay: $F(2,52) = 0.293$; sex \times habituation: $F(1,52) = 0.781$; delay \times habituation: $F(2,52) = 0.732$; sex \times delay \times habituation: $F(2,52) = 0.445$]. The numbers of choices of the correct screen were significant with the 30-s [$t(21) = 5.504$; $P < 0.001$] and the 60-s [$t(19) = 2.088$; $P < 0.001$] delays, but not with the 120-s delay [$t(21) = -0.299$; n.s.].

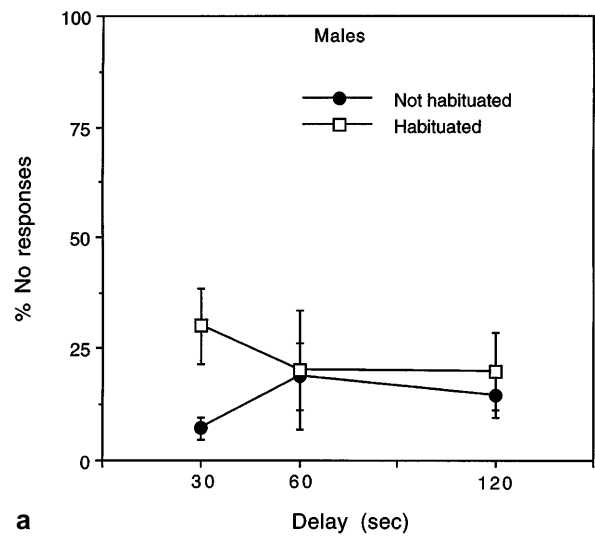
Percentages of invalid trials are shown in Fig. 7. The ANOVA revealed a significant sex \times habituation interaction [$F(1,52) = 5.273$; $P = 0.0257$]; however, separate analyses for males and females showed no significant effects of habituation [$F(1,26) = 2.604$; $P = 0.119$; $F(1,26) = 2.888$; $P = 0.101$, respectively]. There were no other statistically significant effects [sex: $F(1,52) = 0.158$; delay:



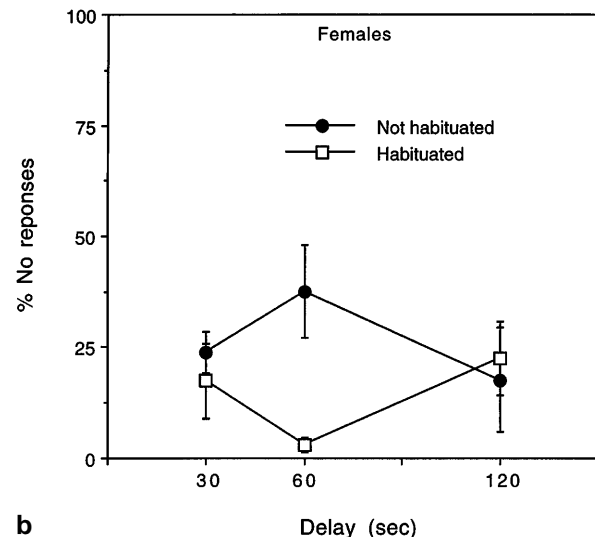
a



b



a



b

Fig. 6a, b Mean percentages (\pm SEM) of choices for the correct screen in experiment 3 in **a** male and **b** female chicks using an opaque partition preventing chicks' sight of the two screens during the delay period. Data are reported both for chicks that had previously (during training) been accustomed to the use of the opaque partition (*habituated*) and for chicks that had never experienced the opaque partition before (*not habituated*)

Fig. 7a, b Mean percentages (\pm SEM) of invalid responses in experiment 3 in **a** male and **b** female chicks using an opaque partition preventing the chicks from seeing the two screens during the delay period. Data are reported both for chicks previously (during training) accustomed to the use of the opaque partition (*habituated*) and for chicks that had never experienced the opaque partition before (*not habituated*)

$F(2,52) = 0.027$; habituation: $F(1,52) = 0.056$; sex \times delay: $F(2,52) = 0.017$; delay \times habituation: $F(2,52) = 2.525$; sex \times delay \times habituation: $F(2,52) = 1.306$].

General discussion

The temporal characteristics of the chicks' representation of an object that has disappeared were investigated by testing chicks' ability to search for the object in the correct spatial location, i.e. where it had last been seen. In experiment 1, chicks were able to correctly orient their search towards the artificial social companion after a delay of up to 180 s from its disappearance behind an obstacle. With longer delays their search became random. In experiment 2, chicks were given an extra cue (the colour and pattern of the screen) which might improve their search strategy, but the availability of the featural cue did not affect chicks' performance. The spatial position of the screens, rather than other characteristics, such as their colour, seemed to be the relevant factor for this task. In experiment 3, the goal was obscured from view throughout the delay by an opaque cover. In this case chicks could still find the correct screen, but only up to a much shorter delay of 60 s, and choices became random for a delay of 120 s. This drop of performance when the opaque partition was used could be explained in several ways. The simplest explanation would attribute the effect to the introduction of a novel and potentially frightening object (the opaque partition) that would affect their emotional state, rather than disturbing their cognitive abilities to detect, remember, and choose the correct location. However, this possibility was disproved by experiment 3, which compared the performances of chicks that were or were not accustomed to the opaque partition. Alternatively, if, during the delay, chicks remain physically oriented towards the correct screen, prevention of visual contact with the environment where the goal was last seen might interfere with orienting responses towards the correct spatial location. No evidence of such a behavioural strategy was observed in our chicks, which kept moving in all directions during the periods of confinement within the transparent cage. Chicks might remain visually oriented towards the screen even when moving in other directions; however, it is virtually impossible to check for their visual orientation, since they could be using both frontal and lateral viewing of both the right and the left eye. The most likely explanation is, therefore, that the presence of the opaque screen might cause interference with chicks' cognitive strategy, if, for example, the sight of the screens is somehow used to rehearse where the imprinting object is to be looked for. Similar effects of the visibility of the test tray during the delay phase have been documented in primates, and have been usually attributed to visual orientation, or to attentional factors associated to visual orientation (Fletcher 1965).

Even when the opaque screen was used during the delay period, the performance of the chicks nonetheless re-

mained impressive. One minute is a very long period of delay, fully comparable in length with the retention intervals observed in mammalian species under similar test conditions (Fletcher 1965; Wu et al. 1986). Retention intervals as long as 100 s have been found in tits (*Parus*) using delayed non-matching-to-sample tasks (Healy 1995), but in this case the tests were very different because they involved specific conditioning procedures, the use of different stimuli from trial to trial, and extensive training. In our procedure the initial training was largely devoted to habituating the animal to the novel environment, because the chicks' response of following the imprinted ball occurs naturally, and, even during testing, the number of trials was quite limited. Obviously, it can be claimed that chicks might rely very little on cognitive and representative skills in this task. They could have simply learnt to associate proximity of the ball to a screen as a cue for direct approach responses towards that screen. Nevertheless, and in particular in the condition in which the screens were not visible, in order to solve the problem, chicks needed to maintain some form of representation of the position of the correct screen, and to continuously update the content of the representation from trial to trial on the basis of the directional cues provided by the movement of the ball. In mammals, the maintenance of information "on-line" during short temporal intervals is usually described as working memory, and is believed to be implemented in some neural circuitry within the prefrontal cortex (Goldman-Rakic 1987; Fuster 1989). An involvement of the prefrontal cortex in Piagetian object-permanence tasks has been suggested for both humans and monkeys (Diamond and Goldman-Rakic 1989; see also Johnson 1997 for a review). There is now evidence that a region resembling the mammalian prefrontal cortex does exist in the avian telencephalon – a semilunar area in the caudalmost part of the forebrain, called the neostriatum caudolaterale (NCL) (see Mogensen and Divac 1982). It has been shown in pigeons that temporary receptor blocking of D1 receptors (which are the prevailing dopamine receptor subtype in the mammalian prefrontal cortex) in the NCL strongly affects working memory while leaving reference memory unimpaired (Güntürkün and Durstewitz 1998). No data are available at present for any involvement of the avian NCL in the delayed response problem, but the issue seems worth investigating.

In the experiments reported here a social, though artificial, goal-object was employed. Virtually all studies on the delayed response problem have used food as the incentive. The only study of which we are aware that used social incentives revealed that the performance of young macaques was as good as or better than the maximum performance levels reported for macaques tested with food incentives (Wu et al. 1986). It would be interesting in future work to compare chicks' performance in the delayed response problem using different types of incentives.

Acknowledgements All experiments and treatment of animals comply with the "Principles of animal care", publication No. 86-23, revised 1985, of the National Institute of Health and with current national (Italian) laws.

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