J Comp Physiol A (1995) 177: 371–378

ORIGINAL PAPER

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Failure of interocular transfer in two types of learning in the crab *Chasmagnathus*

Accepted: 4 February 1994

Abstract Crabs (*Chasmagnathus granulatus*) were trained monocularly and then tested after 24 h, in order to study interocular transfer (IOT) in two habituation paradigms. 1) Habituation of the escape response to an iterated visual danger stimuli. Monocular crabs exhibited retention after 24 h when trained and tested with the same uncovered eye, but not with different uncovered eyes. 2) Habituation of the exploratory activity to a novel environment. This long term habituation of the exploratory activity is exhibited after 24 h in monocular animals trained and tested with the same uncovered eye but not with different uncovered eyes. An explanation of this failure of IOT will be discussed in terms of retrieval impairment due to a) a different perception of training and testing stimuli, b) lateralization of memory storage, or c) the existence of two symmetrical, independent and redundant lateral storage sites.

Key words Interocular transfer · Memory processing · Habituation · Crabs · Lateralization

Introduction

If an animal that learns to respond to a visual stimulus presented to only one eye can continue to respond accurately when the stimulus is presented to the other eye, it is said to exhibit interocular transfer (IOT) (Wehner and Müller 1985). IOT is an important phenomenon relating to mechanistic aspects of acquisition and retention of long-term memory. The occurrence of IOT is shown to depend on the following factors: a) the degree of difficulty in a task to be learned (Muntz 1961; Schulte 1957; Menkhaus 1957; Ingle 1968), b) the amount of training given on a particular discrimination problem (Catania 1963), c) the type of response required from the subject (McClearly 1960), d) the specific stimuli employed (Ingle 1965), e) the experimental paradigm used (Green et al. 1978), f) the amount of crossed and uncrossed retinal projections in vertebrates (Robinson 1982; Cowie and Parkinson 1973; Ingle 1965; Van Hof 1970; Cowan et al. 1961; Sharma 1972; Mohn and Steele Russell 1983) or g) the position of the discriminated stimuli on the retina (Levine 1945; Graves and Goodale 1977; Mallin and Delius 1983).

In vertebrates, mainly in birds, a number of studies aimed at assessing IOT have demonstrated that monocular testing may reveal hemispherical lateralization and brain asymmetries in visual perception and memory (Sherry et al. 1981; Rogers 1986; Clayton 1992a; Clayton and Krebs 1993, 1994), suggesting in addition, that the memory traces are not stably stored at the sites of their original registration but that are rather gradually transferred to different neural locations (Tiunova 1994; Clayton 1992a; Clayton and Krebs 1993, 1994b). In studies with invertebrates, the desert ant *Cataglyphis* exhibits no IOT when it uses landmarks for orientation but complete transfer when the insect navigates by the pattern of polarized light in the sky. The former result has been understood as indicating some contribution from monocular mechanisms peripheral to binocular convergence, while the latter, as suggesting that the locus of the function would be downstream from the place where information from the two eyes is combined (Wehner and Müller 1985). Thus, studies on transfer of visual information using monocular occlusion, could contribute to elucidate the localization of the memory trace.

Two learning paradigms have been extensively studied in the crab *Chasmagnathus granulatus* during the last years, namely, long-term habituation of the

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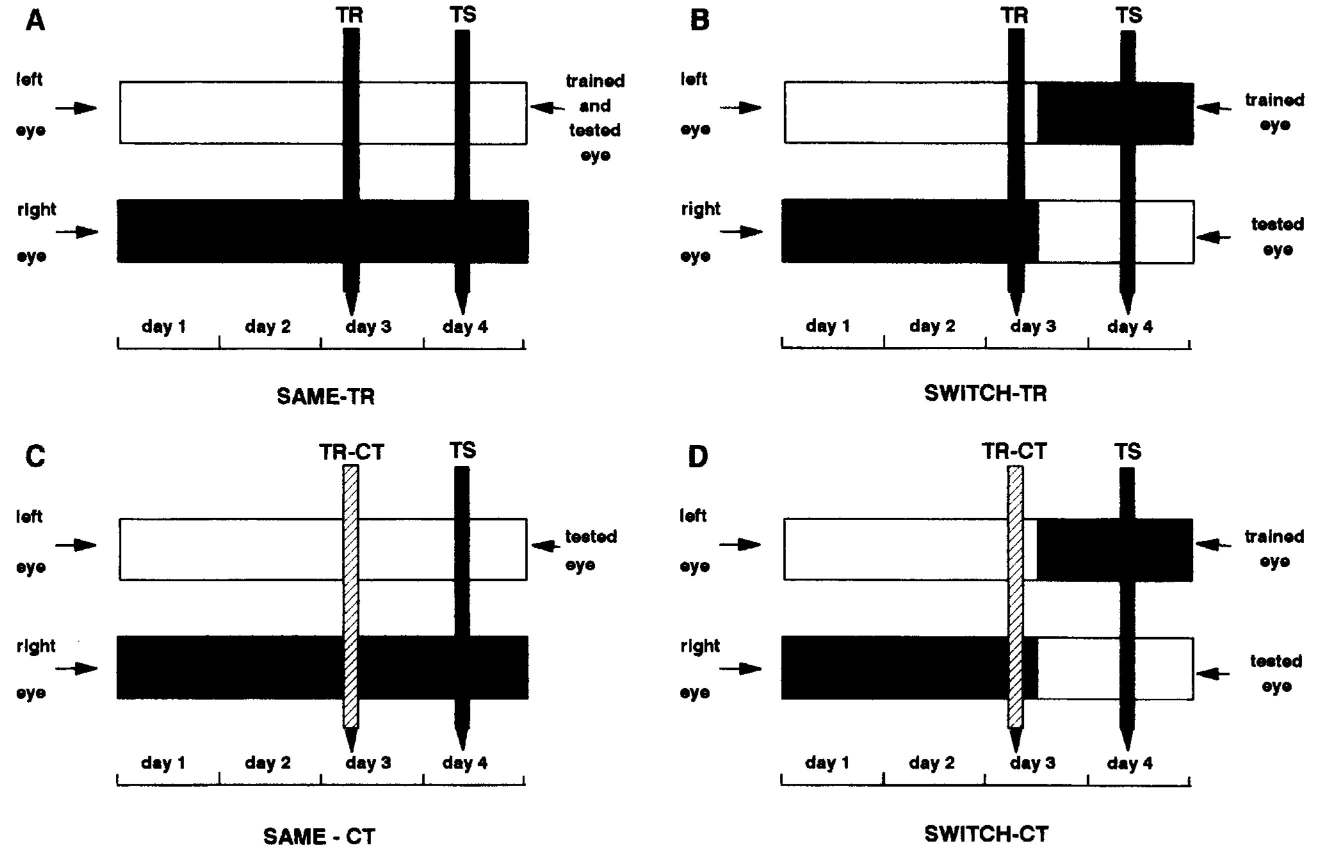

Fig. 1A–D Experimental design: *Horizontal bars* stand for left and right eyes; *black bars*: covered eye; *white bars*: uncovered eye. *Full arrows*: *TR*: training session; *TS*: testing session. *Hatched arrow*: *TR-CT*: Animals are placed in the experimental device but no actual training occurs

escape response to a visual danger stimulus, and long-term habituation of the exploratory behavior to a novel environment (e.g. Brunner and Maldonado 1988; Maldonado et al. 1989; Lozada et al. 1990; Dimant and Maldonado 1992; Hermitte 1994). Both memory processes are based on visual information which seems to be mainly processed in the optic lobes, two extremely lateralized masses of nervous tissue that account for a significant part of the brain (Sandeman 1990). The aim of this research at our laboratory is to study localization and kinetics of the memory trace in these processes. As part of such approach, the present work was conducted to ascertain whether or not IOT occurs in both learning paradigms.

Material and methods

Animals

Animals were adult male *Chasmagnathus* crabs 2.6–2.9 cm across the carapace, collected from water less than 1 m deep in the *rias* (narrow coastal inlets) of San Clemente del Tuyú, Argentina, and transported to the laboratory, where they were lodged in plastic tanks (35 × 48 × 27 cm) filled to 2 cm depth with water, at a density of 35 crabs per tank. Water used in tanks and other containers during experiments was prepared with hw-Marinex (Winex-Germany) (salinity 0.10–0.14%, pH 7.4–7.6). The Holding room was maintained on a 12 h light-dark cycle (light on 07: 00–19: 00 h). Animals were fed rabbit pellets (Nutrientes SA, Argentina) every 3 days and after feeding the water was changed. Temperature of both holding and experimental rooms as well as the alley between them was maintained within a range of 19–24°C.

Experiments were carried out within the first week after the animal's arrival and between November and June (i.e. late spring, summer and fall). Each crab was used only in one experiment.

Before animals were appointed for an experiment, they underwent a *selection test*: each crab was turned on its back and only animals that immediately returned to their normal position were used. The rationale behind this selection is that crabs with a slow righting reaction show a low responsiveness to a large diversity of stimuli, and at a later time, they usually present unhealthy symptoms. No more than 10% of tested crabs were eliminated.

Experimental design

To test IOT the animals were trained after covering one of the eyes with a light–tight black elastic strip (10 mm × 30 mm) cemented dorsally (prothoraxic region) and ventrally (sub-orbital region) on the carapace (DAY 1, Fig. 1A, B). All the animals were then kept in their home tanks for 48 h and trained on DAY 3. After training was complete the strip from the naive eye was removed and either replaced over the same eye (SAME-TR, Fig. 1A) or switched to the trained eye (SWITCH-TR, Fig. 1B). All the animals were then kept in their home tanks for 24 h and tested on DAY 4. During testing, the performance of trained groups (SAME-TR, SWITCH-TR; Fig. 1A, B) was compared between them and with the control groups, which though having experienced monocular occlusion had not been trained (SAME-CT, SWITCH-CT; Fig. 1C, D).

Two learning paradigms

Long-term habituation of the escape response. The apparatus is described in detail elsewhere (Romano et al. 1990). Briefly, the experimental unit was the *actometer*: a bowl-shaped plastic container with a steep concave wall and a circular central flat floor 10 cm diameter, covered to a depth of 0.5 cm with water. The crab was placed in the container which was suspended by three strings from an upper wooden framework (23 x 23 x 30 cm) and illuminated by a 10 W lamp fixed 30 cm above the animal. An opaque rectangle screen (a strip of 25 x 7.5 cm) could be moved horizontally by a motor over the animal and across the upper surface of the framework in 2.3 s. Screen displacements provoked a crab's running response and consequently container oscillations. A stylus was centrally cemented to the bottom of the container and connected to a piezoelectric transducer. Container oscillations induced, through the transducer, electrical signals proportional to the velocity of the oscillations (Cady 1964). Such signals were amplified, integrated during the recording time (9 s) and translated into numerical units ranging from zero to 1530, before being processed by computer. Thus, the scores were correlated proportionally to the velocity and number of the container oscillations recorded during 9 s. The amplification of the voltage changes was kept at such a gain that scores remained below 1530. The experimental room had 40 actometers, isolated from each other by partitions.

A computer was employed to program trial sequences, trial duration and intertrial intervals, as well as to monitor experimental events.

Trained crabs (SAME-TR and SWITCH-TR) received a training session of 30 trials with 180-s intertrial intervals. Control animals (SAME-CT and SWITCH-CT) were kept in the actometers during the entire training session but without screen presentation. The testing session had 2 trials. Each trial lasted 9 s and consisted of passing the screen 4 times over the actometer, recording the crab's activity during the entire trial time. Crabs were individually housed, during the intersession interval, in plastic containers covered to a depth of 0.5 cm with water and kept inside drawers dimly lighted. Both training and testing session were preceded by a 15-min adaptation time in the actometers.

Long-term habituation of exploratory activity. The apparatus is described in detail elsewhere (Dimant and Maldonado 1992). Each experimental unit (the *choice-chamber*) consisted of a plastic box (25 x 25 x 15 cm) divided in two compartments of equal size (25 x 12.5 x 15 cm) by a central partition: the dark compartment (DC) and the light compartment (LC). DC had its walls painted black and a removable roof that prevented stray light from entering. LC was illuminated by a 10 W lamp and had its wall painted white. A sliding door in the central partition, which could be raised or lowered by a motor, allowed a crab to pass from DC to LC or vice versa. The floor of DC was covered by a 0.5 cm deep layer of water, and a 1 cm high door step prevented the solution from entering LC. Absence of water in LC did hindered not influence the crab's mobility in the choice chamber, while its presence in LC the operation of the sliding door. An infrared emitter–receptor system (ER), mounted on an arcade-like device, was located in LC. A computer monitored the sliding door and recorded the interval elapsing between the moment when the door was raised and when the infrared beam was first interrupted by the crab. This time interval is called the *latency value*. Forty such choice-chambers were set up in the isolated experimental room.

Twenty-four hours before the animals were monocularly occluded, they were numbered on their backs with white paint. For the training session, trained crabs (SAME-TR and SWITCH-TR) were moved from their home tanks and individually placed in DC of the choice-chambers with the sliding doors close. After 10 min of adaptation time, the doors were raised, crabs entered LC, their first latencies were recorded and then, they were allowed to explore the choice-chamber for 2 h. Control crabs (SAME-CT and SWITCH-CT) were individually housed in circular plastic transparent cylinders (18 x 16 cm) deprived of internal partitions and evenly illuminated, which they were allowed to explore for 2 h. During the entire intersession interval, both trained and control crabs were collectively housed in the home tanks and then underwent a 4-trial testing session in the choice-chambers. During each testing trial, animals were placed in DC and after 10 m of adaptation time, the doors were raised and latencies to enter LC were recorded.

Data analysis and evaluation of memory retention

Long-term memory was assessed by focusing the data analysis on testing scores. Rescorla (1988) argued convincingly in favor of using this type of analysis instead of a paired training-testing comparison, stressing the need to distinguish clearly between *time of input* (training session) and *time of assessment* (testing session).

To compare mean training scores an ANOVA of repeated measures was performed.

Interocular transfer was assessed with a Duncan Multiple Range Comparisons performed on testing data of the four groups, namely, SWITCH-TR, SWITCH-CT, SAME-TR and SAME-CT.

Results

Habituation of the escape response

Pilot experiments with bilaterally blinded crabs showed that animals do not respond at all to the movement of the opaque screen speaking for the effectiveness of the occlusion technique.

A first experiment was carried out to compare the performance of binocular and monocular animals in a paradigm of long-term habituation to the repeated presentation of a visual stimulus (the opaque screen passing overhead in the actometer). One group of 66 crabs had both eyes uncovered (BI-group) and another one of the same number had one eye occluded (MO-group). Half of the animals in each group underwent a 30 trial training session (TR-groups), 180 s intertrial interval, and the other half remained in the actometers during the time corresponding to the training session (2 h), but without being stimulated by the passing screen (CT-groups). Thus, four groups of 33 crabs each were obtained and named: BI-CT, BI-TR, MO-CT and MO-TR. A 2-trial testing session took place after a 24-h intersession interval.

Results are shown in Fig. 2. Performance of trained groups (BI-TR and MO-TR) during the 30-trial training session exhibit a similar profile though the response level of binocular crabs was sharply higher than that of monocular ones (Fig. 2A). A 2 x 15 ANOVA of repeated measures of 2-trial block data disclosed significant main and trial effects [$F(1, 64) = 18.45$; $P < (0.05)$ and $F(14, 896) = 2.25$; $P < (0.05)$, respectively, but not group x trial interaction [$F(14, 896) = 0.58$]. A Duncan test on data corresponding to the 2-trial testing session (Fig. 2B) revealed a significant difference both for binocular (BI-CT vs BI-TR) and monocular groups (MO-CT vs MO-TR), and both between trained groups

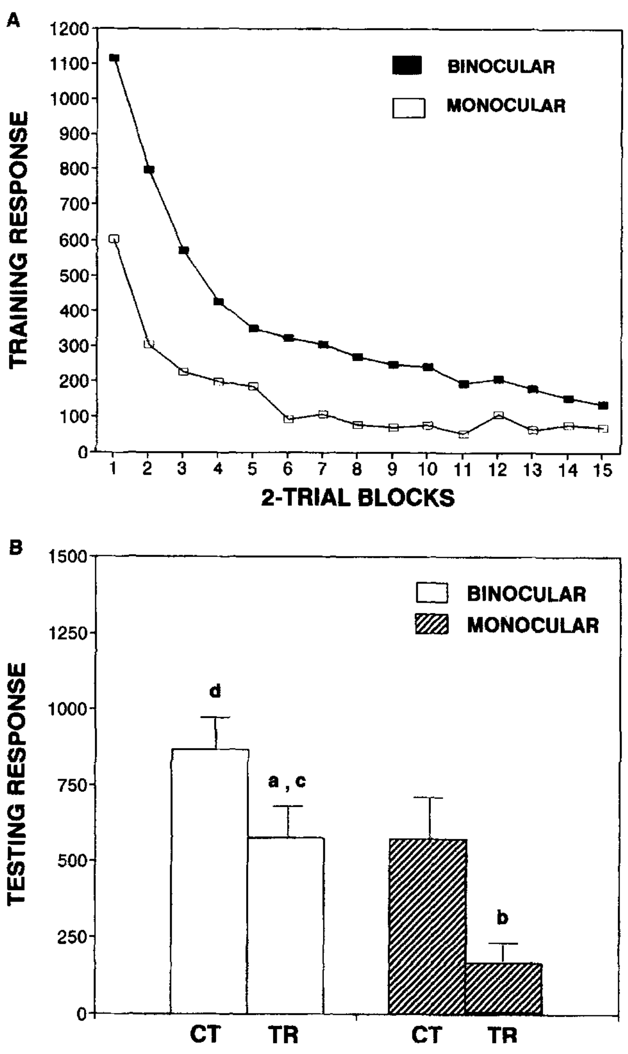

Fig. 2A, B Acquisition and retention of long term habituation to a visual danger stimulus in binocular (both eyes uncovered) and monocular (one eye uncovered) crabs ($n = 33$). **A** Training session. *Ordinate*: 2-trial blocks response scores. **B** Testing session. *CT*: control groups, *TR*: trained groups. Duncan test: *d* $P < 0.05$ for MO-CT VS BI-CT, *a* $P < 0.05$ for BI-CT vs BI-TR, *c* $P < 0.01$ for BI-TR vs MO-TR, *b* $P < 0.005$ for MO-CT vs MO-TR. *Ordinate*: 2-trial blocks response scores

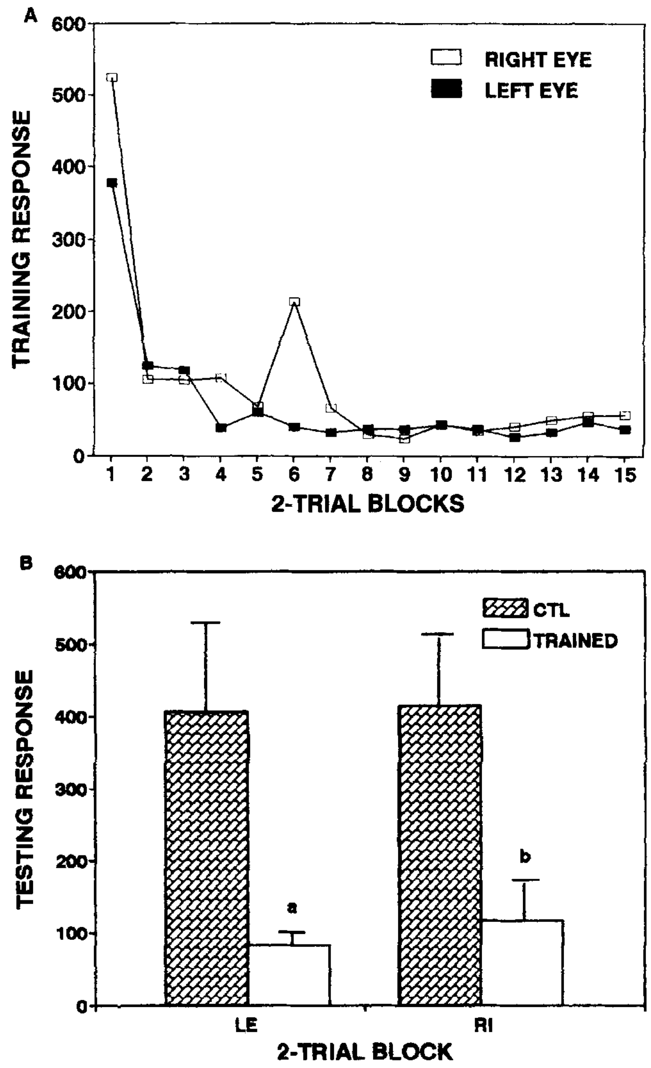

Fig. 3A, B Acquisition and retention of long term habituation to a visual danger stimulus in monocular crabs ($n = 40$). **A** Training session. **B** Testing session. *LE*: left eye uncovered in training and testing; *RI*: right eye uncovered in training and testing. Duncan test: *a* $P < 0.05$ for LE-TR vs LE-CT; *b* $P < 0.05$ for RI-TR vs RI-CT. *Ordinates* as in Fig. 2

(BI-TR vs MO-TR) and between control groups (BI-CT vs MO-CT).

Thus monocular crabs, as binocular ones, can build up a long-term habituation to an iterated visual stimulus, in spite of showing a clearcut lower response level during training. This result suggests that habituation does not depend either on the response level, a view supported by several previous works (Peeke 1984; Tomsic et al. 1991), or on the formation of a central "binocular" image.

To test whether or not monocular crabs can acquire the habituated response regardless of the eye used during training, a second experiment was performed. One group of 80 monocular animals had the right eye uncovered (RI-groups) and another group of 80 animals had the left eye uncovered (LE-groups). Half of the animals in each group underwent the usual 30-trial session (TR-groups) and the other half were not trained (CT-groups). Accordingly, four groups of 40 crabs each were formed and named: RI-TR, RI-CT, LE-TR and LE-CT. A 2-trial testing session was carried out after 24 h.

Results are displayed in Fig. 3. A 2×15 ANOVA of repeated measures on 2-trial block training scores (Fig. 3A) showed neither significant main effect nor group × trial interaction ($F(1, 78) = 1.46$ and $F(14, 1092) = 0.67$, respectively). A Duncan multiple range test on data of testing (Fig. 3B), revealed

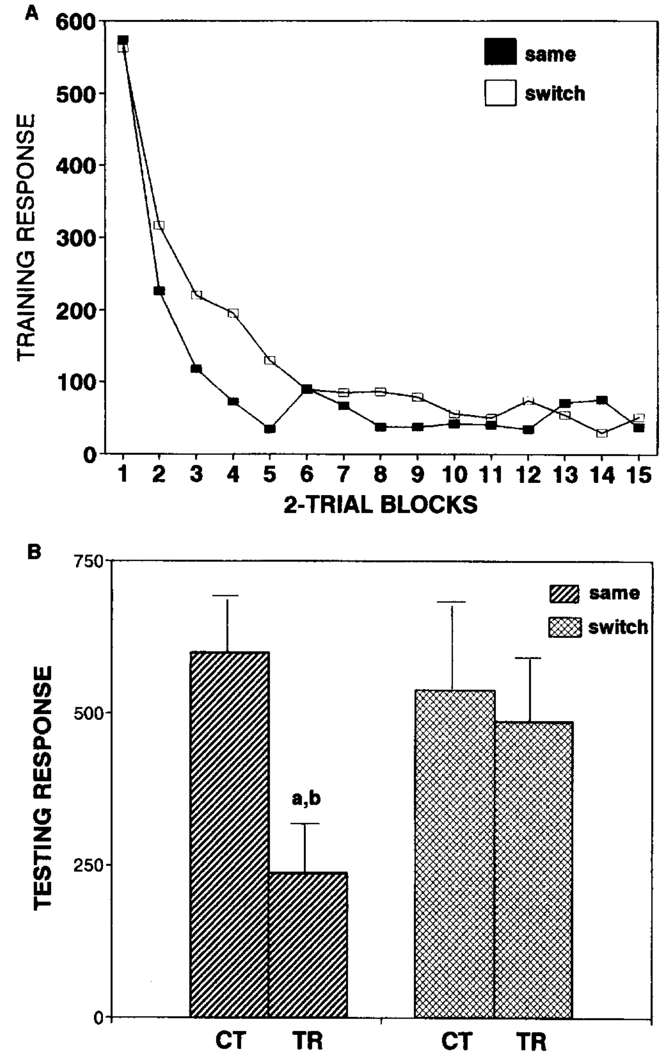

Fig. 4A, B Acquisition and retention of long term habituation to a visual danger stimulus in crabs trained and tested with the same uncovered eye (*SAME*) or with different uncovered eyes (*SWITCH*, left in training and right in testing) ($n = 40$). **A** Training session. **B** Testing session. Duncan test: *a* $P < 0.05$ for SAME-TR vs SAME-CT, *b* $P < 0.05$ for SAME-TR vs SWITCH-TR. *Ordinates* as in Fig. 2

a similar significant retention for both RI-TR and LE-TR groups respectively, but no significant difference between control or trained groups.

Therefore, crabs seem to acquire the habituated response with either trained eye.

In the following experiment the design described in Fig. 1 was adopted. Namely 160 monocular animals were distributed in 4 groups of 40 each and were named: SAME-CT, SAME-TR, SWITCH-CT and SWITCH-TR. A training-to-testing interval of 24 h was used.

A 2 × 15 ANOVA of repeated measures of 2-trial block data of SAME-TR and SWITCH-TR at training showed neither a significant between-group difference nor a group × trial interaction [$F(1, 78) = 1.04$ and $F(14, 1092) = 0.16$], respectively, (Fig. 4A). A Duncan test on data of the 2-trial testing session (Fig. 4B), disclosed a significant difference either for SAME-CT vs SAME-TR or between trained groups (SAME-TR vs SWITCH-TR), but not significant difference either for SWITCH-CT vs SWITCH-TR or between controls (SAME-CT vs SWITCH-CT).

Thus, long-term retention of the habituated response is shown when crabs are tested with the trained eye but not with the naive eye. In other words, no IOT is exhibited by the crab *Chasmagnatus* in long-term habituation to an iterated visual danger stimulus.

Habituation of the exploratory activity

The habituation of the escape response and that of exploring activity share the condition of both being habituation processes but differ in the target behavior, namely, the former implies a decline in a defensive reaction while the latter in exploratory activity; one implies habituation to a visual danger stimulus and the other habituation to novelty (Dimant and Maldonado 1992). Given such notable differences, the purpose of experiments in this section was to test whether failure of IOT is also found in exploratory habituation.

Experiments were conducted using the choice-chamber. The group formation was as above, that is, there were four groups of 40 monocular crabs each, termed: SAME-CT, SAME-TR, SWITCH-CT and SWITCH-TR. During the 2-h training session, trained crabs (TR-groups) explored the choice-chamber while controls (CT-groups) explored the plastic transparent cylinders. After a 24-h training-to-testing interval, all the animals underwent the 5-trial testing session in the choice chamber. The latency of each trained crab corresponding to its first entering to LC was recorded.

Results was exhibited in Fig. 5A. Similar performance were observed during training. A t-test on the mean training scores of these groups showed no significant differences ($t = 0.67$). In contrast, a Duncan test performed on data of the 3-trial testing session (Fig. 5B), disclosed a significant difference either between SAME-CT and SAME-TR or between trained groups (SAME-TR and SWITCH-TR), but no significant difference either between SWITCH-groups or between controls (SAME-CT vs SWITCH-CT).

These results together with those from the previous section seem to support the conclusion that IOT is not exhibited in long-term habituation, either of the escape response or of the exploratory activity.

Discussion

We failed to find interocular transfer in either learning paradigms tested in the crab *Chasmagnathus*

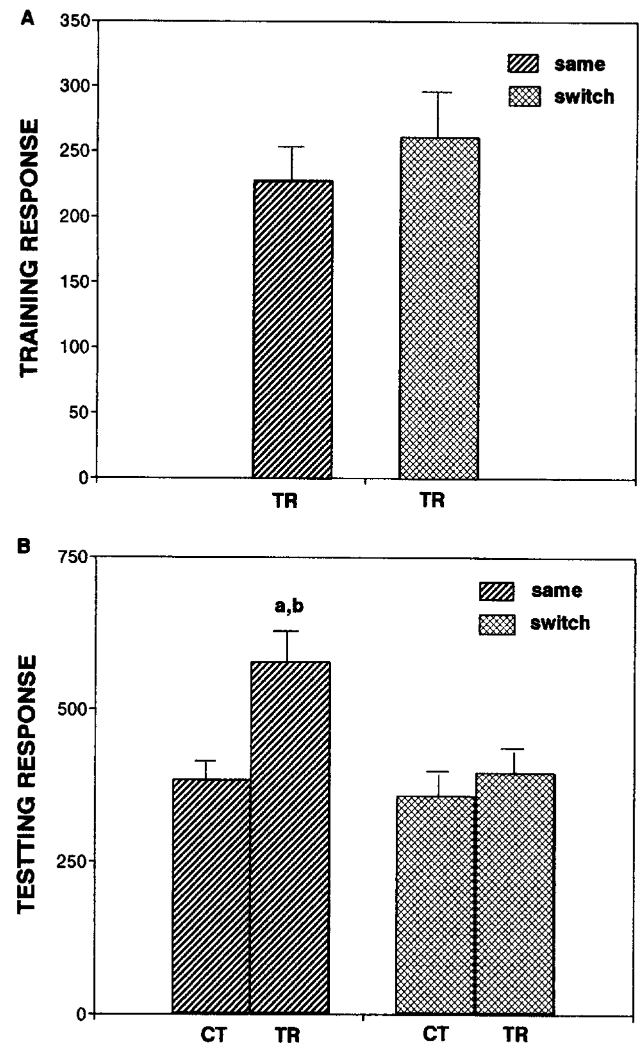

Fig. 5A, B Acquisition and retention of long term habituation of exploratory behavior in crabs trained and tested with the same uncovered eye (*SAME*) or with different uncovered eyes (*SWITCH*, left in training and right in testing) ($n = 40$). **A** Training session. **B** Testing session. Duncan test: a $P < 0.01$ for SAME-TR vs SAME-CT, b $P < 0.01$ for SAME-TR vs SWITCH-TR. *Ordinates*: Latency to enter LC

granulatus. Three hypotheses may be suggested to account for these results.

First, testing performance when crabs use the naive eye could be simply the result of using different eyes during training and testing. Under this hypothesis, IOT cannot be discarded. Retrieval impairment may result as a consequence of poor congruence between encoding and retrieval stimuli Peck and Ader 1974; Santucci and Riccio 1986; Spear 1973, 1978). However two lines of evidence appear not to support this explanation.

a) Either right- or left-monocular crabs show similar latencies to enter LC in the choice-chamber, similar exploratory behaviour (Hermitte 1994) and comparable profiles of the training curves in habituation of the escape response (Fig. 3). This latter result is specially relevant since any time that the disparity between stimuli proved to be sufficiently large, clearcut differences in the training curves' profiles were found (Romano et al. 1991; Rakitin et al. 1991).

b) Binocular crabs shown generalization in both paradigms even when sharp differences between training and testing stimuli are provided (Hermitte 1994; Lozada 1994).

Thus it seems unlikely that a disparity in the visual perception of the two eyes could account for the failure to find IOT.

According to a second hypothesis, the outcome of the present experiments may be interpreted as evidence of failure to find IOT (Sherry et al. 1981). Memories formed by one eye system would not be accessible to the contralateral system because each eye system attends to different types of memory. Most relevant to this approach are the studies of Rogers (1986), Andrew (1988, 1991), Rashid and Andrew (1989), Mench and Andrew (1986) and Clayton and Krebs (1994a) in avian species.

A different type of lateralization in birds has also been suggested (Rogers 1986; Graves and Goodale 1977 and Clayton and Krebs 1994a) that would also render lack of IOT. One hemisphere would suppress the other one via some arrangement of interhemispheric coupling in order to minimize a conflict that would impair performance. In experiments of the present paper no differences in the performance of both types of monocular crabs were found (Fig. 2A, B). These results do not rule out the possibility of an interlateral inhibition because any potential competition between memories was prevented by monocular training, thereby allowing only one kind of memory to be stored (Rogers 1986; Gaston and Gaston 1984; Clayton and Krebs 1994a).

Further, recent studies on lateralization in birds, (Clayton 1992; Clayton and Krebs 1993, 1994b), showed retention after 24 h, only in monocular animals tested with the right eye uncovered, even when that eye was covered during training, indicating that memory once accessible to left eye becomes available only to the right eye and only in the food storing species. Regarding our experiments with crabs, results suggest that this type of lateralization is not likely to be present, at least after 24 h, since no IOT was found in the SWITCH-group and performance of both SAME-groups was equally good.

It is worth noting a difference concerning the functional significance attributed to lateralization in birds and crabs. In birds, it is assumed to prevent conflict of information arising from the visual input of laterally placed, independent (largely monocular) eyes with little binocular overlap. This may not be the case in crabs, whose eyes placed at the top of two peduncles are endowed of widespread movements probably producing a significant binocular overlap.

The third explanation is based on the work with the desert ant *Cataglyphis* (Wehner and Müller 1985) on interocular transfer. The locus of the visual memory for both learning processes described so far, may indicate the contribution from monocular mechanisms peripheral to binocular convergence. Therefore, when a monocular crab is tested with the naive eye it could not use the information which entered through the other eye and was stored in the contralateral optic lobe. However, monocular animals could either use the information stored in the ipsilateral locus if trained and tested with the same eye, or use an integrated memory if trained binocularly. In other words, it is assumed that crabs acquire two identical monocular memories, each recalled independently by stimuli entering through the respective eye. There would be two symmetrical eye systems playing the same role and thus mnemonic mechanisms would be redundant. This hypothesis does not deny binocular convergence of visual information but assumes it is not involved in the engram.

Further experiments are required in order to test which of these hypotheses are correct.

If there is no IOT and the last hypothesis is fitting, then one might predict that memories formed with one eye should be as accurate as binocular memories, that is, retention tested with both eyes uncovered should be equally robust either when one, or both eyes are used during acquisition.

A further point to be investigated concerns the persistence of memory trace in its original place of storage. A kinetic study of the visual memory trace as that performed with birds is required. Such research could elucidate whether the putative system of two monocular memories involves stores definitively separated; or whether the information is unilaterally transferred with a rather slow time course (Clayton 1992; Clayton and Krebs 1993).

Electrophysiological recordings from the optic lobe (Nalbach 1990) and from the visual interneurones in the optic nerve (Wiersma and Yamaguchi 1966, 1967; Glantz 1977) could provide a valid contribution to our understanding of where the putative monocular memories are localized.

Finally, one important point is that lateralization should be examined thoroughly by binocular training and monocular testing in order to exclude an explanation in terms of suppression or competition between two different storing locations.

Acknowledgements This work was supported by the Consejo Nacional de Investigaciones Cientıficas y Técnicas de Argentina, grant PID 216-89 and by the University of Buenos Aires, grant Ex-134. Antorchas. The authors are deeply indebted to Angel Vidal for technical assistance.

References

Andrew RJ (1988) The development of visual lateralization in the domestic chick. Behav Brain Res 29: 201–209

Andrew RJ (1991) The nature of behavioural lateralization in the chick. In: RJ Andrew (ed) Neural and behavioural plasticity. Oxford University Press, Oxford, pp 536–554

Brunner D, Maldonado H (1988) Habituation in the crab *Chasmagnathus granulatus*: effect of morphine and naloxene. J Comp Physiol A 162: 687–694

Cady WG (1964) Piezoelectricity. Dover, New York

Catania AC (1963) Techniques for control of monocular and binocular viewing in the pigeon. J Exp Anal Behav 6: 627–629

Clayton NS (1992) Lateralization and unilateral transfer of spatial memory in marsh tits. J Comp Physiol A 171: 807–815

Clayton NS, Krebs JR (1993) Lateralization in Paridae: comparison of a storing and a non-storing species on a one-trial associative memory task. J Comp Physiol A 171: 779–806

Clayton NS, Krebs JR (1994a) Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 174: 371–379

Clayton NS, Krebs JR (1994b) Lateralization and unilateral transfer of spatial memory in marsh tits: are two eyes better than one? J Comp Physiol A 174: 769–773

Cowan WM, Adamson L, Powell TPS (1961) An experimental study of the avian visual system. J Anat 95: 545–562

Cowie A, Parkinson AM (1973) Effects of sectioning the corpus callosum on interocular transfer in hooded rats. Exp Brain Res 18: 433–445

Dimant B, Maldonado H (1992) Habituation and associative learning during exploratory behavior of the crab (*Chasmangnathus*). J Comp Physiol A 170: 749–759

Gaston KE, Gaston MG (1984) Unilateral memory after binocular discrimination training: Left hemisphere dominance in the chick? Brain Res 303: 190–193

Glantz RM (1977) Visual input and motor output of the command interneurons in the defense reflex pathway of the crayfish. In: (ed. G. Hoyle) Identified neurons and behavior of arthropods. New York, Plenom pp 259–274

Graves JA, Goodale MA (1977) Failure of interocular transfer in the pigeon (*Columbia livia*). Physiol Behav 19: 425–428

Green L, Brecha N, Gazzaniga MS (1978) Interocular transfer of simultaneous but not successive discriminations in the pigeon. Animal Learn Behav 6(3): 261–264

Hermitte G (1994) Papel de las claves en el aprendizaje asociativo en el cangrejo *Chasmagnathus granulathus*. Doctoral Thesis, Universidad de Buenos Aires

Ingle JD (1965) Interocular transfer in goldfish: Color easier than pattern. Science 149: 1000–1002

Ingle JD (1968) Interocular integration of visual learning by goldfish. Brain Behav Evol 1: 58–85

Levine J (1945) Studies in the interrelations of central nervous structures in binocular vision: I. The lack of bilateral transfer of visual discriminative habits acquired monocularly by the pigeon. J Gen Psychol 67: 105–129

Lozada M (1994) Habituación a large término y especificidad del estímulo en el cangrejo *Chasmagnathus granulatus*. Doctoral Thesis, Universidad de Buenos Aires

Lozada M, Romano A, Maldonado H (1990) Long term habituation to a danger stimulus in the crab *Chasmagnathus granulatus*. Physiol Behav 47: 35–41

Maldonado H, Romano A, Lozada M (1989) Opioid action on response level to a danger stimulus in the crab *Chasmagnathus granulatus*. Behav Neurosci 103: 1139–1143

Mallin HD, Delius JD (1983) Inter- and intraocular transfer of color discriminations with mandibulation as an operant in the head-fixed pigeon. Behav Analysis Lett 3: 297–309

McCleary RA (1960) Type of response as a factor in interocular transfer in the fish. J Comp Physiol Psychol 53: 311–321

Mench JA, Andrew RJ (1986) Lateralization of a food research task in the domestic chick. Behav Neural Biol 46: 107–114

Menkhaus I (1957) Versucne über einäugiges Lernen und Transponieren beim Haushuhn. Z Tierpsychol Forsch 14: 210–230

Mohn G, Steelle Russell I (1983) Visual discrimination learning under conditions of interocular conflict in hooded and albino rats. Behav Brain Res 7: 371–378

Muntz WRA (1961) Interocular transfer in *Octopus vulgaris.* J Comp Physiol Psychol 54: 49–55

Nalbach HO (1990) Visually elicited escape in crabs. In: Wiese K, Krenz WD, Tautz J, Reichert H, Mulloney B (eds) Frontiers in crustacean neurobiology. Birkhäuser, Basel Boston Berlin, pp 165–173

Peck JH, Ader R (1974) Illness-induced taste aversion under states of deprivation and satiation. Anim Learn Behav 2: 6–8

Peek HVS (1984) Habituation and the maintenance of territorial boundaries. In: Peeke HVS. Petrinovich L (eds) Habituation, sensitization and behavior. Academic Press, New York, pp 393–421

Rakitin A, Tomsic D, Maldonado H (1991) Habituation and sensitization to an electrical shock in the crab *Chasmagnathus.* Effect of background illumination. Physiol Behav 50: 477–487

Rashid M, Andrew RJ (1989) Right hemisphere advantage for topographical orientation in the domestic chick. Neuropsychologia 27: 937–948

Rescorla RA (1988) Behavioral studies of Pavlovian conditioning. Annu Rev Neurosci 1: 329–352

Robinson SR (1982) Interocular transfer in a marsupial: the brushtailed possum (*Trichosurus vulpecula*). Brain Behav Evol 21: 114–124

Rogers LJ (1986) Lateralization of learning in chicks. Adv Study Behav 16: 147–189

Romano A, Lozada M, Maldonado H (1990) Effect of naloxone pretreatment on habituation in the crab *Chasmagnathus granulatus.* Behav Neural Biol 53: 113–122

Romano A, Lozada M, Maldonado H (1991) Non-habituation processes affect stimulus specificity of the response-habituation in the crab *Chasmagnathus granulatus.* Behav Neurosci 105: 542–552

Sandeman D (1990) Structural and functional levels in the organization of decapod crustacean brains. In: Wiese U, Krenz WD, Tautz J, Reichert H, Mullonay B (eds) Frontiers in crustacean neurobiology. Birkhäuser, Basel Boston Berlin pp 223–239

Santucci AC ,Riccio DC (1986) Hypothermia-induced anterograde amnesia and its reversal in rats trained on a T-maze task. Physiol Behav 36: 1065–1069

Schulte A (1957) Transfer und Transpositionsversuche mit monokular dressierten Fischen. Z Vergl Physiol 39: 432–476

Sharma SC (1972) The retinal projections in the crayfish: An experimental study. Brain Res 39: 213–223

Sherry DF, Krebs JR, Cowie RJ (1981) Memory for the location of stored food in marsh tits. Anim Behav 29: 1260–1266

Spear NE (1973) Retrieval of memory in animals. Psychol Rev 80: 163–175

Spear NE (1978) The processing of memories: Forgetting and retention. Erlabum, Hillsdale, NJ

Tiunova AA (1994) Interocular memory transfer after monocular visual discrimination learning in chicks. In: European Science Foundation (ed) Neuronal mechanisms of learning and memory. Localization and formation of memory trace. Il Ciocco, pp PB18.

Tomsic D, Maldonado H (1990) Central effect of morphine pretreatment on short and long-term habituation to a danger stimulus in the crab *Chasmagnathus.* Pharmacol Biochem Behav 36: 787–793

Tomsic D, Maldonado H, Rakitin A (1991) Morphine and GABA: effects on perception, escape response and long-term habituation to a danger stimulus in the crab *Chasmagnathus.* Brain Res Bull 26: 699–706

Van Hof MW (1970) Interocular transfer in the rabbit. Exp Neurol 26: 103–108

Wehner R, Müller M (1985) Does interocular transfer occur in visual navigation by ants? Nature 315 (6016): 228–229

Wiersma CMG, Yamaguchi T (1966) The neuronal components of the optic nerve of the crayfish as studied by single unit analysis. J Comp Neurol 128: 333–358

Wiersma CAG, Yamaguchi T (1967) Integration of visual stimuli by the crayfish central nervous system. J Exp Biol 47: 409–431