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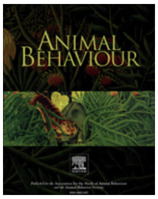

Visual recognition of conspecifics in the American lobster, *Homarus americanus*

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For years, individual recognition has been the subject of many studies but, owing to the intrinsic complexity of the phenomenon, it has also been the source of much controversy. The sensory channel(s) used for recognition has also been much discussed. In aquatic invertebrates, vision has been one of the least understood media. We carried out two laboratory experiments using 49 pairs of adult male American lobsters. The first experiment was aimed at investigating the sensory channel/s (smell, sight or the two combined) used by lobsters to get information about the opponent, whereas in the second experiment we tested whether visual experience might allow lobsters to recognize the familiar opponent. Previous exposure to the sight of a conspecific induced lobsters either to avoid the opponent or to skip preliminaries (approaches and threats) and escalate the interaction. However, such changes in the dynamics of fighting were shown only when the opponent was the individual that the experimental lobster had previously seen rather than a generic lobster. This is the first study to provide evidence that lobsters can identify familiar conspecifics by sight, although this does not necessarily mean that they recognize them as individuals. Further studies are needed to clarify this issue.

The ability to recognize conspecifics (individual recognition) is a critical skill for many animal species (Tibbetts & Dale 2007), being a key element in almost all social networks (reviewed in Zayan 1994). During individual recognition, the recognizer (or receiver) learns the distinctive 'signature' (Beecher 1982) of another individual (the signaller), associates it with specific information about the signaller, and, based on this association, classifies the other as a rival, friend, neighbour, mate, offspring or sibling (Tibbetts & Dale 2007).

In recent years, many studies, using various contexts and taxa, have shown that individual recognition is much more widespread than previously thought (Tibbetts et al. 2008). Many examples are reported in Tibbetts & Dale (2007). Sheep, *Ovis aries*, can recognize parents and offspring on an individual basis (Searby & Jouventin 2003); temperate-breeding hooded warblers, *Wilsonia citrina*, can remember their neighbours from the previous breeding season even after having overwintered in the tropics (Godard 1991); and yellow-bellied marmots, *Marmota flaviventris*, are able to assess the reliability of alarm calls based on the identity of the caller (Blumstein et al. 2004).

The intrinsic complexity of individual recognition, on the one hand, and the wide diversity in its expression, on the other, however, have generated a debate around the defining features of the process (Barrows et al. 1975; Brooks & Falls 1975; Barnard & Burk 1979; Falls 1982; Halpin 1986; Sherman et al. 1997; Steiger & Müller 2008; Tibbetts et al. 2008). A dichotomy between 'true' individual recognition and 'class-level' or 'binary' individual recognition has been proposed. In 'true' individual recognition (Beecher 1989; Tibbetts & Dale 2007), the receiver learns the individually distinctive characteristics of the signaller and associates these characteristics with individual-specific information about it. For example, Tibbetts (2002) showed that the paper wasp *Polistes fuscatus* can identify individual nestmates by unique facial features, as well as we humans recognize our own companions. In contrast, in the 'class-level' (Tibbetts & Dale 2007) or 'binary' individual recognition (Gherardi & Tiedemann 2004), the receiver associates the learned characteristics of the signaller with inferred class-specific information or matches the signaller's phenotype to an internal template associated with different classes (but see Steiger & Müller 2008). For example, while fighting with a conspecific, the hermit crab *Pagurus longicarpus* behaves following the simple rule: 'if I know the opponent, behave as before; if I do not know it, attack' (Gherardi & Tiedemann 2004). Since the present study was not originally designed to solve the issue, we provisionally refer here to individual recognition sensu lato.

Among other social contexts, aggression certainly favours the evolution of individual recognition. The intervention of individual

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recognition may reduce the costs inflicted by agonistic competition and at the same time brings considerable benefits to both the signaller and the receiver (Tibbetts & Dale 2007). For instance, if a territory-holder remembers its neighbour and modulates its responses towards it, its aggressive efforts can be focused on nonterritorial individuals instead of on its 'dear enemy': the energetic costs of territorial defence are thus considerably reduced (Temeles 1994). Individual recognition also has a documented role in the maintenance of dominance hierarchies (Barnard & Burk 1979), as shown in chacma baboons, *Papio cynocephalus ursinus* (Cheney et al. 1995) and bonnet macaques, *Macaca radiata* (Silk 1999), but also in fish (*Oncorhynchus mykiss*: Johnsson 1997), insects (the wasp *Polistes fuscatus*: Tibbetts 2002; the ant *Pachycondyla villosa*: D'Ettorre & Heinze 2005), and a number of decapods (the lobster *Homarus americanus*: Karavanich & Atema 1998; the hermit crab *Pagurus longicarpus*: Gherardi & Tiedemann 2004; and the crayfish *Cherax dispar*: Seebacher & Wilson 2007; and *Cherax destructor*: Van der Velden et al. 2008). In the context of dominance hierarchies, the role of individual recognition should be relevant when the group is small and relatively stable: in this circumstance, it allows a group, in a noncheatable way, to assess the agonistic quality of its members. In a larger group in which familiarity may be limited to a few individuals, an animal may eavesdrop on fighting conspecifics and then make use of transitive inference to gauge the aggressive status of unfamiliar individuals, as shown in the African fish *Astatotilapia burtoni* (Grosenick et al. 2007). In contrast, individual recognition is not effective when groups are particularly large and unstable and are characterized by rare or occasional interactions among their members: in these instances, dominance hierarchies may be maintained only by other, apparently simpler mechanisms, such as (1) the recognition of the opponent's dominance status as denoted by a pheromone, a posture or a behaviour controlled by the signaller's internal state ('status recognition'; Barnard & Burk 1979) or (2) the influence of past social experience in the form of 'winner and loser effects' (Dugatkin & Earley 2004).

The American lobster, *Homarus americanus*, is a highly aggressive species (e.g. Scrivener 1971; Tamm & Cobb 1978; O'Neill & Cobb 1979; Atema & Cobb 1980; Atema & Steinbach 2007). Before the formation of dominance hierarchies, agonistic interactions in this species escalate from stereotyped visual displays to physical contact sometimes leading to limb loss and bleeding (Atema & Voigt 1995; Huber & Kravitz 1995; Atema & Steinbach 2007). Hierarchies are then maintained through a form of individual recognition (Atema & Steinbach 2007): the losers of a previous fight will not challenge a known winner, but will do so with an unfamiliar conspecific, even if the latter is the recent winner of another fight (Karavanich & Atema 1998).

Notwithstanding the abundant literature on the matter, the proximate mechanisms of the agonistic behaviour of *H. americanus* are not completely understood. Lobsters are known to emit stimuli of different types, including tactile, hydrodynamic and acoustical ones (e.g. Breithaupt & Tautz 1990; Henninger & Watson 2005); however, the large majority of studies on this taxon have analysed the chemical substances released and their role in communication with a focus on the hydrodynamics of urine-borne substances (Karavanich & Atema 1991; Berg et al. 1993; Atema & Steinbach 2007) and on their reception (Atema & Steinbach 2007). Sight has often been little studied, mainly because lobsters are nocturnal animals (Cooper & Uzmann 1980; Chabot et al. 2001). However, the agonistic repertoire of *H. americanus* comprises a large number of stereotyped visual displays (e.g. Atema & Voigt 1995; Atema & Steinbach 2007) and its superposition eyes seem to be highly dark adapted (Waterman 1961; Atema & Voigt 1995), suggesting the involvement of vision.

To test the hypothesis that vision plays a role in lobster agonistic behaviour and in individual recognition, we conducted two experiments. The first experiment investigated the sensory channel/s (sight, smell or the two combined) used by lobsters to get information about the opponent. The second explored whether previous visual experience might allow a form of individual recognition.

METHODS

Study Animals

A total of 98 *H. americanus* adult males were obtained from the wholesale trade company Metro Italia Cash and Carry S.p.A. (outlet in Florence, Italy). In the laboratory, each animal was weighed using an electronic scale (to the nearest 0.1 g) and was individually marked with differently shaped plastic tags attached to its carapace with a superglue gel. The length of the cephalothorax, from the tip of the rostrum to the posterior edge of the carapace, was measured using an electronic calliper (to the nearest 0.1 mm). Weight and cephalothorax length ranged between 479 and 517 g and between 11.3 and 11.8 cm, respectively.

Experimental Design and Apparatus

We conducted experiment 1 between 10 June and 18 September 2008 and experiment 2 between 16 March and 12 June 2009. The experimental lobsters were maintained for at least 2 weeks in communal plastic tanks (140 × 110 cm and 100 cm deep) at the density of ca. 18 individuals/m^2 at a water temperature of 13.5–14.0 °C. Claws were immobilized with elastic bandages to prevent injuries; claw immobilization did not appear to cause stress or abnormal behaviour in the lobsters. Each tank contained 500 litres of artificial (Instant Ocean salt) sea water (salinity: 33.3%) and was provided with a recirculating 500 litre pump, four air pumps, a protein skimmer and 20 clay pots as shelter. Since *H. americanus* is mainly nocturnal (MacKenzie & Moring 1985) and the laboratory was available only during the day, lobsters were induced to reverse their day:night cycle of activity. To do so, for 2 weeks (a period shown to be sufficient to reverse the rhythm of *H. americanus*; Goergen et al. 2000), the experimental lobsters were trained to an artificial light:dark cycle (approximately 14:10 h) with lights off at 0600 and lights on at 2000 hours. Lobsters were fed ad libitum with fish and cuttlefish minced meat. Tanks were cleaned daily using a hose and 25% of water was renewed twice a week.

The experimental lobsters were then released from the bandages on their chelae and kept isolated for 2 weeks in a fibreglass aquarium (60 × 40 cm and 50 cm deep) containing 80 litres of artificial sea water as above, filtered by a recirculating 100 litre pump and provided with two air pumps, a protein skimmer and a clay pot as shelter. During isolation, lobsters were not exposed to the putative status recognition odours and isolation was sufficiently long to allow lobsters to forget both the individuals previously met and social odours (Karavanich & Atema 1998). Feeding and cleaning of the aquaria followed the same procedure as in the maintenance.

The experiment was conducted at low-intensity red light, to which lobsters are scarcely sensible (sensitivity is greatest near 525 nm, blue-green light; Kennedy & Bruno 1961; Kampa et al. 1963). Experiments started at 0800 hours (i.e. 2000 hours for the experimental lobster) on a total of 49 pairs of males, matched for body length (±1.5%) and weight (±2.5%). Each pair was randomly assigned to one of the seven treatments/controls described below, reaching a total of seven replicates per treatment/control. Lobsters were used only once to avoid pseudoreplication. The experimental