zoology

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

Table 1
Behavioural patterns recorded, the corresponding types of agonistic interaction, and the score assigned to each type of interaction (modified after Atema & Voigt 1995)

Behavioural pattern	Description	Type of interaction, score
Tail-flip escape	A contraction of the abdomen which propels the lobster backwards for a rapid escape	Avoidance, 0
Retreat	A lobster moves or turns away from an opponent	
Approach	A lobster advances towards an opponent slowly reducing the distance to less than a body length	Approach, 1
Lunge	Rapid and direct head-first advance towards opponent(s) without hesitation, often with claws outstretched	
Antennae up	Both antennae are pointed straight up and away from the opponent	Threat, 2
Antennae tap	In a single motion, an antenna is rapidly swept downwards over the anterior portion of the thorax of the opponent	
Antennae whipping	One of both antennae vigorously and repeatedly lash the opponent in rapid sequence	
Stand off	Complete stillness other than antennal movements, less than a body length apart	
Claw up	One or both claws are lifted high above the horizontal and extended laterally	
Claw down	One or both claws are pointed straight down towards the substrate	
Threat	Aggressive display, claws extended outwards and upwards	
Claw touch closed	A lobster touches the opponent with closed claws	Strike, 3
Claw touch open	A lobster touches the opponent with open claws	
Chase	Rapid pursuit of retreating opponent	
Push/pull/punch	A lobster attempts to displace an opponent through pushing and pulling using walking legs and pleopods and/or uses claws to push and/or punch claws or body of the opponent	
Claw grasp	A lobster uses its claws to grab an appendage of the opponent	Fight, 4
Claw rip	A rapid motion in which a lobster grasps the opponent and pulls at it quickly	
Claw strike	A lobster strikes towards the opponent with one or both of its claws	
Claw stretch	Claws interlocked with opponent, forward stretch of one claw while other claws defends against opponent's outstretched claw	
Scissor	Rapid scissoring motion with both claws at opponent	
Tail-flip	Contraction of the abdomen to propel animal backwards in an attempt to rip off opponent's appendage	

apparatus consisted of fibreglass tanks (80 × 80 × 80 cm) with a rough bottom containing 256 litres of artificial sea water as above; each tank was divided in half by a removable divider and was provided with a recirculating 500 litre pump, four air pumps and a protein skimmer.

The experiment consisted of two phases lasting 30 min each: 'familiarization' and 'fight'. In the familiarization phase of experiment 1, the two males were allowed (in the Treatments) or not allowed (in the Control) to smell ('Smell only'), see ('See only') or smell and see ('Smell and See') each other. The Control and the Treatments differed in the type of divider used: it was (1) opaque and not drilled in the Control, (2) opaque and finely drilled with holes (diameter: 7 mm; density: 9 per cm^2) in Smell only; (3) transparent and not drilled in See only; and (4) transparent and drilled as in (2) in Smell and See. Before the 'fight' phase, each lobster was placed back in its individual aquarium for the time needed to wash the experimental tank to remove any possible odour. The two lobsters in each pair were then put back in their original half of the experimental tank and allowed to acclimatize for 10 min, the divider was removed and the fight phase commenced.

Because experiment 1 showed that prior visual experience significantly altered lobster behaviour (see Results), we designed experiment 2 to test whether recognition might be visual in this species. To investigate this, we first allowed the lobsters to see each other during a 30 min familiarization phase in the same tank as in the Treatment 'See only'. Then, we followed the same procedures as in experiment 1, but, before putting the lobsters into the experimental tank, we switched one of the two lobsters from seven pairs, randomly chosen, with a lobster from a different pair that had been subjected to the same protocol (Treatment 'Unfamiliar Opponents'). All the experimental tanks were identical, in both size and shape, as were all the other conditions, so we can exclude any bias from the different familiarity of the lobsters with the tank. We compared the unfamiliar pairs' behaviour with that of seven pairs of lobsters subjected to the same manipulation as unfamiliar pairs except being switched (Treatment 'Familiar Opponents'). The same Control ($N = 7$) as in experiment 1 was also run. At the end of each trial, the experimental apparatus was again washed thoroughly with clean tap water.

Data Collection

We videotaped the behaviour of the lobsters during the experimental phase of both experiments, using an infrared CCD camera, activated at a distance to avoid disturbance to the experimental animals. The camera was mounted on an articulated iron beam suspended directly above the experimental tank and connected with a VCR. A code number was given to each tape for subsequent blind reading. The tapes were examined in random order by an experienced observer who did not know the experimental design or our expectations.

During the familiarization phase, we recorded the total time (s) spent by lobsters both in locomotion and in executing two types of agonistic interactions, that is, approach and threat (see below and Table 1), and the number of approaches to the divider. Following Cenni et al.'s (2010) definition, an agonistic interaction was classified as an encounter between two individuals starting when an opponent approaches the other and ending when an opponent retreats or tail-flips away at the distance of one body length for at

Table 2
Experiment 1: familiarization phase

	Control	Smell only (SM)	See only (SE)	Smell and See (SS)	*F*/*H*	*P*	Post hoc
Time spent in locomotion (s)	276.12 (20.94)	363.96 (27.43)	685.30 (12.39)	697.76 (13.93)	399.94	**<0.001**	SS=SE>SM=Control
Time spent in approach (s)	25.69 (11.80)	30.29 (8.63)	51.07 (15.38)	54.07 (18.53)	387.78	**<0.001**	SS=SE>SM=Control
Time spent in threat (s)	6.14 (3.08)	6.64 (2.13)	11.69 (3.94)	12.79 (4.83)	376.44	**<0.001**	SS=SE>SM=Control
Number of approaches	8.85 (1.84)	9.88 (1.92)	19.57 (1.29)	19.28 (1.84)	20.77	**<0.001**	SS=SE>SM=Control

The table shows mean values (standard error in parentheses) of the time that *H. americanus* spent in locomotion, approach and threat, and mean numbers of approaches to the divider in the Control and in the Treatments. Control and Treatments consisted of adult males not allowed to smell/see an opponent (Control) or allowed to smell only (Treatment SM), see only (Treatment SE) or smell and see (Treatment SS) the opponent. Comparisons were made using a generalized linear model (F, $df = 3, 2$) and Kruskal–Wallis test (H, $N = 7$), followed by post hoc analyses, i.e. Tukey tests and multiple comparisons tests, respectively. Sample size is 7 for each Control and each Treatment. Significant values are denoted in bold.

Table 3
Experiment 2: familiarization phase

Experiment 2	Control	Familiar Opponents (FO)	Unfamiliar Opponents (UO)	*F*/*H*	*P*	Post hoc
Time spent in locomotion (s)	278.45 (18.146)	698.65 (12.81)	689.45 (10.21)	201.23	**0.05**	FO=UO>Control
Time spent in approach (s)	25.79 (11.08)	51.93 (18.66)	52.05 (17.43)	211.31	**0.05**	FO=UO>Control
Time spent in threat (s)	7.01 (4.03)	13.01 (3.88)	12.78 (3.48)	200.65	**0.05**	FO=UO>Control
Number of approaches	7.65 (1.24)	19.81 (1.26)	18.89 (2.02)	14.35	**0.01**	FO=UO>Control

The table shows mean values (standard error in parentheses) of the time that *H. americanus* spent in locomotion, approach and threat, and mean numbers of approaches to the divider in the Control and in the Treatments. Control and Treatments consisted of adult males not allowed to smell/see an opponent (Control) or allowed only to see the opponent (Treatments Familiar Opponents, FO, and Unfamiliar Opponents, UO). Comparisons were made using a generalized linear model ($F, df = 3, 2$) and Kruskal–Wallis test ($H, N = 7$), followed by post hoc analyses, i.e. Tukey tests and multiple comparisons tests, respectively. Sample size is 7 for each Control and each Treatment. Significant values are denoted in bold.

least 10 s without the other one pursuing. Approach and threat, together with avoidance, strike and fight, are arranged in a taxonomy of agonistic interactions based on their intensity (Table 1; Atema & Voigt 1995): avoidance (one individual retreats with no overt act by the other); approach (one individual advances towards the other); threat (one individual retreats when the other raises its chelae); strike (individuals execute agonistic behavioural patterns of low intensity, i.e. touches and pushes); and fight (individuals execute agonistic behavioural patterns of high intensity). In the Treatment 'Smell only', the behavioural patterns lunge and claw up/down, even if not necessarily oriented towards the opponent, were classified as components of approaches and threats, respectively. A score was assigned to each of them, as detailed in Table 1.

During a 'fight' we recorded the number of agonistic interactions, the average maximum agonistic level (obtained by summing all the scores in each trial and dividing this value by the total number of the agonistic interactions), and the percentage of dominance (i.e. the fights won by the dominant divided by the overall number of fights, as a percentage). We deemed as dominant the individual that won more than 50% of the fights, following the criterion used in the decapod literature (e.g. Gherardi & Cioni 2004). The winner was the individual that did not retreat or that retreated after the opponent had assumed a body down posture or remained motionless.

Statistics

Data were first checked for normality and homogeneity of variance using the Kolmogorov–Smirnov and Levene tests, respectively, which allowed us to use parametric tests when appropriate. The time spent in locomotion and the average maximum agonistic level were analysed by one-way ANOVAs, followed by Tukey tests. The time spent in approach and threat was compared among treatments by fitting a generalized linear model (GLM), in which the treatments and the type of agonistic interaction were entered as fixed factors. For the other parameters, nonparametric tests were used. In particular, the number of approaches to the divider, the number of agonistic interactions and the percentage of dominance were compared using the Kruskal–Wallis test in both experiments, followed by multiple comparisons tests. Except for the number of agonistic interactions and the percentage of dominance, the analyses were done on the values averaged between the two lobsters per pair. The level of significance under which the null hypothesis was rejected is $\alpha = 0.05$. All tests are two tailed.

Ethical Note

The experiments comply with the current laws of Italy, the country in which they were done. Individuals were maintained in appropriate laboratory conditions to guarantee their welfare and responsiveness. We intended to separate the lobsters and consider the observation over if fights appeared to escalate to potentially damaging levels, but this never happened. After the experiments were completed, the lobsters were killed by hypothermia; they were kept at −20 °C for 1 week.

RESULTS

Familiarization Phase

In experiment 1, the lobsters that were allowed to see the rival, independent of whether they were able to smell it, spent more time in locomotion, threat and approach than the lobsters that could only smell it or that were tested in the Control (Table 2). The sight of the rival made them more prone to approach the divider.

As expected, in experiment 2, lobsters behaved in the same way at the sight of the rival in both Treatments ('Unfamiliar' and 'Familiar Opponents'; Table 3, Fig. 1a).

Fight Phase

The lobsters that had been allowed to see the rival during the familiarization phase of experiment 1 (Treatments 'See only' and 'Smell and See') reached a significantly higher agonistic level than in the Treatment 'Smell only' and in the Control, whereas agonistic interactions were less frequent and shorter (Table 4). Specifically, the time spent in approach and threat (but not in avoidance, strike and fight) was shorter and the percentage of dominance reached significantly higher values.

In experiment 2, the lobsters interacted more often and for longer when the rivals were unfamiliar rather than familiar. In

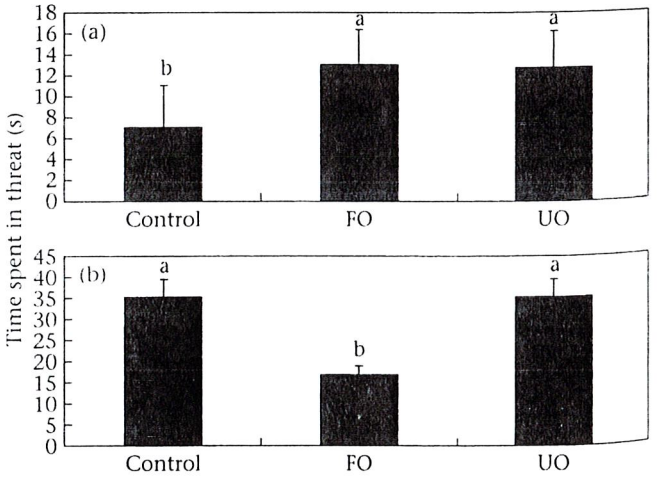

Figure 1. Experiment 2: time (mean + SE) spent by the experimental lobsters in threat posture during (a) the familiarization phase and (b) the fight phase in the Control and in Familiar Opponents (FO) and Unfamiliar Opponents (UO) treatments. Letters over bars denote significant differences at $P < 0.05$, after a GLM followed by a post hoc Tukey test. Control and each treatment were replicated seven times.

Table 4
Experiment 1: fight phase

	Control	Smell only (SM)	See only (SE)	Smell and See (SS)	*F*/*H*	*P*	Post hoc
Time spent in avoidance (s)	2.79 (0.921)	5.71 (0.691)	8.79 (0.648)	9.00 (1.35)	9.664	**0.001**	SS=SE>SM=Control
Time spent in approach (s)	49.11 (4.23)	46.07 (4.95)	25.29 (2.30)	20.79 (3.15)	12.779	**0.001**	SS=SE<SM=Control
Time spent in threat (s)	35.73 (4.19)	32.36 (4.08)	16.93 (1.89)	15.43 (2.72)	9.491	**0.001**	SS=SE<SM=Control
Time spent in strike (s)	18.34 (2.62)	15.43 (2.26)	10.36 (2.14)	17.79 (2.39)	2.62	0.06	SS=SE=SM=Control
Time spent in fight (s)	10.02 (1.28)	10.50 (1.69)	8.43 (1.87)	11.14 (2.28)	0.397	0.776	SS=SE=SM=Control
Number of interactions	41.27 (4.63)	36.93 (3.94)	24.57 (3.32)	21.29 (2.98)	19.464	**0.001**	SS=SE<SM=Control
Mean max. agonistic level	1.61 (0.28)	1.75 (0.19)	1.99 (0.11)	2.06 (0.03)	4.406	**0.008**	SS=SE>SM=Control
Dominance (%)	56.2 (5.12)	57.6 (4.17)	65.3 (3.56)	66.7 (2.77)	24.657	**0.001**	SS=SE>SM=Control

The table shows mean values (standard error in parentheses) of the time spent by *H. americanus* in avoidance, approach, threat, strike and fight, and mean numbers of interaction and of the maximum agonistic level and percentage of dominance of the winner for each pair, in the Control and in the Treatments. Treatments Smell only (SM), See only (SE), Smell and See (SS) and the Control consisted of adult males that in the familiarization phase had been or not allowed to smell and/or see an opponent as indicated in Table 2. Comparisons were made using a generalized linear model (F, $df = 3, 2$) and Kruskal–Wallis test (H, $N = 7$) followed by post hoc analyses, i.e. Tukey tests and multiple comparisons tests, respectively. Sample size is 7 for each Control and each Treatment. Significant values are denoted in bold.

addition, when interacting with familiar conspecifics, the lobsters' average maximum agonistic level was significantly lower, as was the time spent in approach and threat, but not in avoidance, strike and fight; the percentage of dominance was significantly higher. Unfamiliar opponents showed the same behaviour as the lobsters tested in the Control (Table 5, Fig. 1b).

DISCUSSION

This study provides the first clear evidence that *H. americanus* relies on vision during agonistic interactions. Since fighting dynamics, dominance and the agonistic level differed significantly between treatments as a consequence of the lobsters' visual familiarity with the opponent, our results also confirm Karavanich & Atema's (1998) finding that *H. americanus* is able to recognize opponents on an individual basis and suggest that vision has a role in this ability. First, we found that, during familiarization, when the two rivals were separated by a transparent divider, lobsters clearly responded to the sight of the conspecific by increasing both the time spent in locomotion and the number of approaches relative to the trials in which the divider was opaque. Second, the sight of the rival during familiarization had the effect of increasing the number of avoidances and decreasing the number of approaches and threats during the fight phase, compared to the lobsters that had previously been allowed only to smell the opponent. In the sight rather than in the odour treatment, agonistic interactions were less frequent but stronger and the winner reached higher values of dominance. Taken together, these results might indicate that the previous exposure to the sight of a conspecific induces lobsters either to avoid the opponent or to skip preliminaries (approaches and threats) and escalate the interaction. However, such changes in fighting dynamics were shown only when the opponent was the individual that the experimental lobster had seen during familiarization and not, other conditions being equal, an unfamiliar one.

At least two hypotheses can be raised to explain these results. We suggest that individual recognition in lobsters is mainly based on sight. As claimed by several authors (e.g. Van der Velden et al. 2008), vision is one of the least understood media used in individual recognition. Colour variation among wolves, *Canis lupus*, and African wild dogs, *Lycaon pictus*, variable, unique patterns in male ruff, *Philomachus pugnax* (Lank & Dale 2001) and blue-headed wrasse, *Thalassoma bifasciatum*, defending territories (Warner 1987), and peculiar egg and nestling coloration in common murres, *Uria aalge* (Gaston et al. 1993) and royal terns, *Sterna maxima* (Buckley & Buckley 1972), respectively, may have evolved to signal identity. Studies on visual individual recognition are limited in invertebrates, although some have helped reveal the importance of vision (Giurfa et al. 2001; Herath et al. 2001; Horridge 2005; Yurkovic et al. 2006). For example, *Polistes* paper wasps are able to identify individual nestmates by unique facial features (Tibbetts 2002) and the crayfish *C. destructor* can recognize familiar individuals based on their facial width or on some other features associated with it (Van der Velden et al. 2008). These results are analogous to the receivers' specialization for facial individual recognition found in humans (Kanwisher & Yovel 2006), rhesus macaques, *Macaca mulatta* (Tsao et al. 2006) and sheep (Kendrick & Baldwin 1987). In other invertebrates, visual recognition has most often been investigated by manipulating some morphological traits. For instance, aggressive behaviour towards a conspecific was found to be affected by modifying with white paint the size of natural white markings on the chelae of *Calcinus laevimanus* (Dunham 1978), altering the body patterns of *Calcinus tibicen* (Hazlett 1972), or attaching identity tags to the carapace of *Potamon fluviatile* (Vannini & Gherardi 1981). Fiddler crabs (*Uca* spp.) can distinguish species and mates when natural patterns are modified with paints and typically approach unpainted unfamiliar rather than familiar conspecifics (Detto et al. 2006).

Table 5
Experiment 2: fight phase

	Control	Familiar Opponents (FO)	Unfamiliar Opponents (UO)	*F*/*H*	*P*	Post hoc
Time spent in avoidance (s)	8.79 (0.648)	34.93 (6.42)	9.29 (2.73)	13.643	**0.001**	FO>UO=Control
Time spent in approach (s)	49.07 (4.95)	25.29 (2.31)	48.93 (4.69)	10.328	**0.001**	FO<UO=Control
Time spent in threat (s)	35.36 (4.108)	16.93 (2.09)	35.21 (4.36)	8.374	**0.001**	FO<UO=Control
Time spent in strike (s)	18.43 (2.26)	18.29 (2.52)	17.69 (2.64)	0.019	0.982	FO=UO=Control
Time spent in fight (s)	10.48 (1.12)	9.86 (2.11)	10.43 (1.68)	0.033	0.967	FO=UO=Control
Number of interactions	40.41 (4.03)	25.25 (3.06)	39.07 (4.25)	9.485	**0.007**	FO<UO=Control
Mean maximum agonistic level	1.61 (0.77)	1.93 (0.08)	1.57 (0.98)	4.505	**0.006**	FO>UO=Control
Dominance (%)	55.9 (4.98)	66.3 (6.02)	56.3 (5.11)	12.834	**0.001**	FO>UO=Control

The table shows mean values (standard error in parentheses) of the time spent by *H. americanus* in avoidance, approach, threat, strike and fight, and mean numbers of interaction and of the maximum agonistic level and percentage of dominance of the winner for each pair, in the Control and in the Treatments. Treatments Familiar Opponents (FO) and Unfamiliar Opponents (UO) and the Control consisted of adult males that in the familiarization phase had been or not allowed to smell and/or see an opponent as indicated in Table 3. Comparisons were made using a generalized linear model (F, $df = 3, 2$) and Kruskal–Wallis test (H, $N = 7$) followed by post hoc analyses, i.e. Tukey tests and multiple comparisons tests, respectively. Sample size is 7 for each Control and each Treatment. Significant values are denoted in bold.

Vision can also be important for the resolution of fights (e.g. Vannini & Gherardi 1981; Bruski & Dunham 1987); aggressive interactions, for example, escalate under decreased light intensity (Bruski & Dunham 1987) and are modulated by visual displays (Heckenlively 1970; Rubenstein & Hazlett 1974). In *C. dispar*, when the claws of the original winners were disabled, the winners kept on winning against the same opponents; this effect disappeared when the previous winners encountered unfamiliar individuals (Seebacher & Wilson 2007).

We hypothesize that chemicals, possibly acting in concert with tactile stimuli and water vibrations (e.g. Breithaupt & Tautz 1990; Henninger & Watson 2005), serve as backup signals to visual stimuli when sight is limited. Most research effort has been directed to study the chemical substances or pheromones emitted during social interactions in aquatic crustacean decapods (Caldwell 1992; Zulandt Schneider et al. 1999; Bergman et al. 2003; Bergman & Moore 2005; Moore & Bergman 2005). These organisms have efficient systems for both delivering and detecting chemical stimuli (e.g. Breithaupt et al. 1999; Breithaupt & Atema 2000). The urine, excreted through the nephropores at the base of the antennae, is an important source of information, not only about identity but also about sex, aggressive motivation and some other attributes (McLeese 1973; Atema 1986; Atema & Cowan 1986; Breithaupt & Atema 2000; Bergman et al. 2003), whereas the antennules are the main organs involved in perceiving chemical stimuli associated with sex (Ameyaw-Akumfi & Hazlett 1975; Dunham & Oh 1992; Bushmann & Atema 1997; but see Belanger et al. 2008), moult state (Atema & Cowan 1986) and dominance status (Karavanich & Atema 1991; Rutherford et al. 1996; Zulandt Schneider et al. 1999, 2001). In lobsters, for example, odours are used by males to identify the sex of a conspecific approaching their shelter and thus to decide whether to accept it (if a female) or to drive it out of the shelter (if a male intruder; Bushmann & Atema 1997).

Alternatively, sight and olfaction may provide different but complementary information that might enhance the accuracy of the signal in a nonredundant system of communication (Johnstone 1996). Indeed, there is increasing evidence that decapods communicate via composite signals, emitted through more than one sensory channel (i.e. multimodal signals; Partan & Marler 2005). For instance, males of the shrimp *Alpheus heterochaelis* respond aggressively to visual stimuli alone, such as an open claw, but not to chemical stimuli alone; however, when the two are combined and the odour is released by a female, aggressive responses are suppressed (Hughes 1996). The same inhibition of aggression was shown in sexually receptive *P. clarkii* females when subjected to both the sight and the smell of a male (Aquiloni et al. 2009); the refined ability of the females of this species to recognize the dominant male after having eavesdropped on two individuals fighting (Aquiloni et al. 2008) seems to rely on the co-occurrence of visual and chemical stimuli emitted by the male (Aquiloni & Gherardi 2010), which also allows for the individual recognition of the dominant, and not for the recognition of a generic winner.

A similar ability for individual recognition has been clearly shown in the present study on *H. americanus*, as a confirmation of the results of Karavanich & Atema (1998). There is no doubt that the list of the decapods other than lobsters in which this ability has been suggested is constantly lengthening (reviewed in Gherardi & Tricarico 2007). However, except for the river crab *P. fluviatile* (Vannini & Gherardi 1981) and the crayfish *C. destructor* (Van der Velden et al. 2008), no previous study has clearly proven that individual recognition in decapods relies on visual stimuli.

In essence, this study has shown for the first time what was possibly expected but never demonstrated, that *H. americanus* uses visual cues to distinguish familiar from unfamiliar conspecifics. Further studies are obviously needed to understand whether the American lobster is capable of either true or class-level individual recognition, how olfaction and vision interact in performing this skill, and the adaptive significance of social recognition in an apparently 'asocial' animal.

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