

Fish can infer social rank by observation alone

Logan Grosenick^{1,2†}, Tricia S. Clement^{1†} & Russell D. Fernald¹

Transitive inference (TI) involves using known relationships to deduce unknown ones (for example, using $A > B$ and $B > C$ to infer $A > C$), and is thus essential to logical reasoning. First described as a developmental milestone in children¹, TI has since been reported in nonhuman primates^{2–4}, rats^{5,6} and birds^{7–10}. Still, how animals acquire and represent transitive relationships and why such abilities might have evolved remain open problems. Here we show that male fish (*Astatotilapia burtoni*) can successfully make inferences on a hierarchy implied by pairwise fights between rival males. These fish learned the implied hierarchy vicariously (as ‘bystanders’), by watching fights between rivals arranged around them in separate tank units. Our findings show that fish use TI when trained on socially relevant stimuli, and that they can make such inferences by using indirect information alone. Further, these bystanders seem to have both spatial and featural representations related to rival abilities, which they can use to make correct inferences depending on what kind of information is available to them. Beyond extending TI to fish and experimentally demonstrating indirect TI learning in animals, these results indicate that a universal mechanism underlying TI is unlikely. Rather, animals probably use multiple domain-specific representations adapted to different social and ecological pressures that they encounter during the course of their natural lives.

Territorial *A. burtoni* males engage in regular aggressive bouts that determine their access to territory and resources. Males that repeatedly lose fights are unable to hold territories and consequently descend in social status. These males display a different morphology from successful territorial males, losing their bright coloration and becoming reproductively dormant^{11–13}. Success in aggressive bouts is therefore crucial to male reproductive fitness, and the ability to infer the relative strength of rivals before engaging them in potentially costly fights should be highly adaptive^{13,14}.

We tested whether bystander males, after observing pairwise fights between rivals, could synthesize this information to make inferences on an overall hierarchy implied by the fights. To do this we used an adaptation² of a classic five-element model developed to test children’s ability to make TIs on asymmetric relationships¹⁵. Each bystander fish saw staged fights between five size-matched males (A to E, where each letter stands for a different rival male). During training, the following staged fights were presented to the bystander: $A+B-$, $B+C-$, $C+D-$ and $D+E-$, where a plus denotes a ‘win’, and a minus a ‘loss’ (for example, in the pair $A+B-$, rival A dominates rival B) (see Methods). These fights, taken together, imply the dominance hierarchy $A > B > C > D > E$.

Each bystander was trained in the central unit of a square tank divided into several visually and chemically isolated units (Fig. 1). Fights were staged by moving one rival into another rival’s unit, and then removing an opaque barrier, making the fight visible to the bystander (the fight $A+B-$ is shown diagrammatically in Fig. 1). Because *A. burtoni* individuals vigorously defend their territory

against intruding rivals, moving one male into a unit defended by another male always resulted in the intruder losing (see Methods). Thus, we could train each bystander on an artificial dominance hierarchy by using animals whose relative status we controlled. This ensured that there were no consistent differences in male abilities or physical characteristics—a potential confounding factor in naturally formed dominance hierarchies^{14,15}.

Bystander males ($n = 8$) were trained for 11 days on pairwise fights implying $A > B > C > D > E$ (see Methods). Then, to assess whether they could make inferences on the implied hierarchy, we tested their preference between rivals that they had never seen together, giving them a choice between rivals A and E (‘AE’) and a choice between B and D (‘BD’). In the staged fights presented to the bystander, A had always won (against B) and E had always lost (to D). A comparison between these hierarchy end points, known in the literature as ‘end anchors’, was therefore included as a baseline assay of bystander preference (because end anchors are known to generate a large, unambiguous response in TI tasks¹⁶). The BD choice assayed for an inference on the hierarchy, because the B and D rivals won and lost the same number of fights during training, and therefore, after appropriate controls for physical and spatial differences, differed only in their relative position in the implied hierarchy (see Methods).

During bystander preference testing, each bystander was placed between the members of one of the novel pairs (either AE or BD) and, after a controlled viewing period, was allowed to swim freely

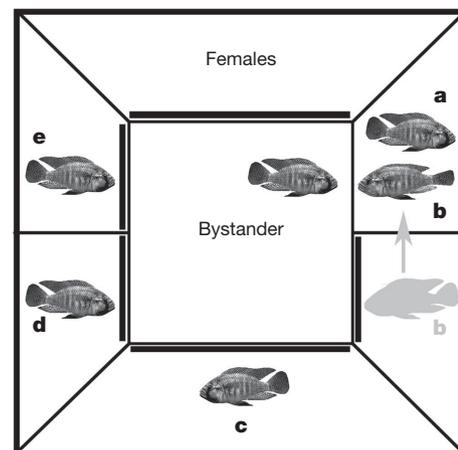


Figure 1 | Tank arrangement and bystander training. Five rival males (A, B, C, D and E) were arranged in visually, chemically and physically isolated compartments around the central bystander unit. To train a bystander on a particular fight, the male scheduled to be the ‘loser’ was removed from its unit and placed in the territory of the scheduled ‘winner’. The opaque barrier separating the bystander from the rivals was then removed to allow the bystander to view the fight. The fight $A+B-$ (A ‘wins’, B ‘loses’) is shown here in diagrammatic form.

¹Department of Biological Sciences, Stanford University, Stanford, California, 94305, USA. ²Center for the Study of Language and Information, Stanford University, Stanford, California, 94305, USA. †Present addresses: Center for the Study of Language and Information, Ventura Hall, 200 Panama Street, Stanford, California 94305, USA (L.G.); eBay, Inc., 2145 Hamilton Avenue, San Jose, California 95125, USA (T.S.C.).

between them. We recorded both the simple binary first-choice result (which rival the bystander approached first) and the overall time spent adjacent to each rival (see Methods). Previous experiments in *A. burtoni*¹⁷ and other fish¹⁴ have shown that time spent in tank quadrants adjacent to a particular male indicates bystander 'preference', and that bystanders spend more time near the rival they perceive to be weaker¹⁴. This is consistent with previous studies of preference in dominance models and, along with our own unpublished findings on *A. burtoni*, motivated our a priori hypothesis that bystanders would prefer the lower-ranking rival in this experiment. Each bystander ($n = 8$) was tested for TI in both the tank where it had seen the staged fights ('familiar context'), and in a tank it had never been in before ('novel context'; see Methods). We tested half the rivals in the familiar context first, and the other half in the novel context first. We used the same AE and BD rivals in both contexts (see Methods).

We used the first-choice results in a general assay for TI, using one-tailed hypothesis testing in the direction of our a priori hypothesis and a significance level of $\alpha = 0.05$. For the AE choice in the familiar context, E was chosen eight out of eight times ($P = 0.004$, binomial), showing that bystanders prefer losing rivals to winning ones here, as expected. In the novel context, however, E was chosen only six out of eight times ($P = 0.14$, binomial). On the critical BD choice, D was chosen seven out of eight times in the familiar context ($P = 0.035$, binomial), and eight out of eight times in the novel context ($P = 0.004$, binomial). Therefore, bystanders chose D as though it were the losing fish, even though (unlike A and E) the B and D rivals differed only in their relative position in the implied hierarchy. Still, this initial evidence on a binary variable was non-significant in one AE context and tells us little about behaviour during preference. We therefore turned to the continuous 'time spent' data to look for subtler effects.

As our sample was too small for appropriate validation of the usual assumptions of parametric significance testing, we used a nonparametric permutation t -test (50,000 replicates) that did not make unverifiable parametric assumptions about the underlying distribution of the data (see Methods). Testing was one-tailed in the direction of our a priori hypothesis, with a significance level of $\alpha = 0.01$. The time spent (T_s) adjacent to each rival was summarized in one score as the difference between time spent near the lower-ranking rival minus the time spent near the higher-ranking rival. Under the null hypothesis that bystanders show no preference for the lower-ranking rival, the expectation of T_s would be less than or equal to zero.

In the A versus E preference test ($n = 8$), T_s was significantly positive in both the familiar context ($P = 0.01$) and the novel context ($P = 0.003$), showing that the bystanders significantly preferred E as expected. In the critical B versus D preference test, T_s was again significantly positive in both the familiar context ($P = 0.003$) and in the novel context ($P = 0.008$), showing a significant preference for the D rival in both contexts (see Fig. 2).

We wondered whether the degree to which one rival dominated over or submitted to other rivals during bystander training had an impact on bystander inference behaviour. Specifically, if the C rival's dominant and submissive behaviour were ambiguous, there might be less social information available to the bystander about the transitive relationship $B > D$ than if the outcomes of the fights were clear (that is, if C very obviously submitted to B and dominated D).

To examine such effects we calculated a 'dominance score' (DS) measuring each rival's dominance/submission behaviour in each fight. Focal observations of five highly correlated behavioural variables known to index dominant and submissive behaviour (chase, flee, bite, threaten, and eyebar activation)¹³ collected from both rivals during each of the 336 fights were subjected to a standard principal-components analysis (PCA). Data projected onto the first principle component then provided a single DS for each rival male in each fight. DS values were more positive for increasing dominant behaviour,

more negative for increasing submissive behaviour, and near zero for ambiguous behaviour (see Methods).

To explore whether rival dominant/submissive activity predicted bystander performance on the BD discrimination, we regressed T_s for the BD preference choice on a combination of C dominant/submissive behaviours as seen by each bystander (combined rival behaviour). Combined rival behaviour was calculated for each bystander from the normalized absolute values of the summed DS values (it therefore indexed overall activity, independently of whether that activity was dominant or submissive; see Methods). Given the number of data points ($n = 8$) and multiple tests, it was decided beforehand that all P values would be Bonferroni-corrected to account for familywise error and then tested at the $\alpha = 0.05$ level (see Methods). We then ran regressions separately for the familiar and novel contexts. Interestingly, we found that while C rival activity during training failed to predict bystander discrimination in the familiar context ($t = -1.271$, $P = 1$ (corrected), $R = 0.461$), it did so to a significant extent in the novel context ($t = 3.896$, $P = 0.048$ (corrected), $R = 0.847$), positively predicting time spent away from B and near D (Fig. 3). Furthermore, a comparison of the regression slopes using repeated-measures analysis of covariance indicated that the two regression slopes were significantly different at the $\alpha = 0.05$ level ($F_{2,12} = 6.50$, $P = 0.012$). Corresponding regressions on B and D rival activity were not significant for either context.

Previous research has shown that fish use redundant coding of spatial and featural information to represent their surroundings¹⁸. We suggest that such redundant representation is behind the pronounced difference in how social information learned by bystanders during training affects their performance in different contexts during testing. In particular, it is clear that when information about the training context was available to them (as in the familiar context), all bystanders were able to make the correct discrimination. However, given only rival featural information (as in the novel context), bystanders showed a linearly graded performance based on how clear fight outcomes involving the transitive element C had been. This strongly suggests that different representations of rival abilities related to learned spatial and featural cues may be used by bystander males, depending on what contextual information is available to them at the time of choice.

The mechanism underlying TI behaviour in animals has been widely debated^{2,4-10,19-25}, and often acts as a proxy for a larger debate between proponents of associative versus cognitive accounts of animal learning and behaviour²⁶. In associative models, TI behaviour is a result of direct reinforcement history. Such models cannot explain the current findings without modification, because vicarious TI involves no direct reinforcement of any kind. Further, the linear relationship observed between transitive C element activity and T_s

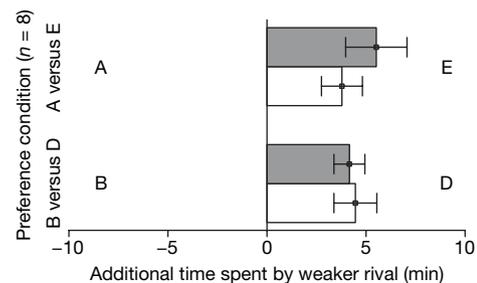


Figure 2 | Time spent near rival males during preference testing. Bar plots of the difference in time spent near the higher-ranking versus the lower-ranking rival (T_s) in the AE (top) and BD (bottom) preference tasks by context. Filled bars, familiar context; open bars, novel context. One-sample permutation t -tests (50,000 replicates) showed that in all cases bystanders spent significantly more time near the lower-ranking rival, namely D or E (AE familiar context, $P = 0.01$; AE novel context, $P = 0.003$; BD familiar context, $P = 0.003$; BD novel context, $P = 0.008$). Error bars indicate s.e.m.

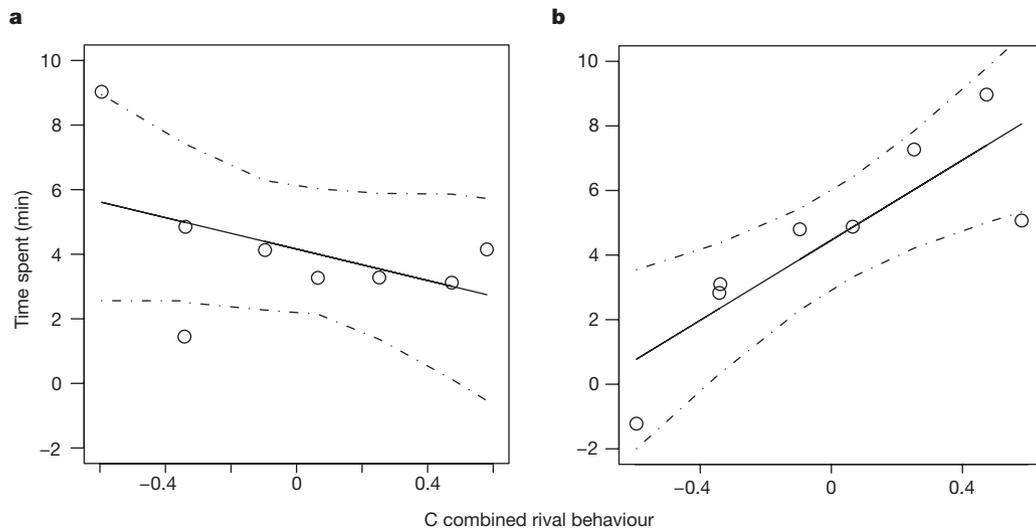


Figure 3 | Time spent during BD preference task as predicted by C combined rival behaviour. **a**, Familiar context; **b**, novel context. T_s , the time spent in the quadrant nearest B minus the time spent in the quadrant nearest D, was regressed on C combined rival behaviour, a measure of overall C rival behaviour during fights. The plots show that whereas C combined rival

behaviour failed to predict T_s in the familiar context ($P = 1$; $R = -0.461$), it did so to a significantly positive extent in the novel context ($P = 0.048$; $R = 0.847$). Both P values have been Bonferroni corrected for multiple comparisons. Dotted lines represent 95% confidence intervals for the line.

in the novel context (when no such relationships were seen for B and D activity) opposes associative 'value transfer' models, in which values associated with B and D would be determined by the behaviour of neighbouring end anchors A and E^{8,20}. We conclude that, at least in this context, a more complex representation is at work.

Last, this instance of the same animal using different representations for TI given different contextual information suggests that considering a single underlying mechanism for TI may not be sufficient. Instead, it seems likely that animals have developed domain-specific representations adapted to the particular social and ecological pressures that they encounter in their natural lives. It has already been established that animals use TI in social settings²⁷, and for *A. burtoni* separate spatial and featural representations underlying TI would be quite consistent with males' different social and ecological needs. In their native habitat in the estuaries and temporary shore-pools of Lake Tanganyika, *A. burtoni* individuals find their established territories regularly disturbed by wind, predation, the movements of hippopotamuses, or the natural changing of the shore-pools^{11,12}. With old territory boundaries destroyed, rival featural representations independent of the altered spatial context would be invaluable—especially because such times of instability have been shown to allow rapid ascent (or descent) in dominance status and therefore in corresponding physiology and reproductive success^{28,29}. Meanwhile, in a stable setting, an additional territorial representation incorporating more than just the degree of rival wins and losses seems to allow more robust TI performance given ambiguous social information—apparently exploiting the spatial acuity of this highly territorial animal.

METHODS

Training tank arrangement, and controls. Rivals ($n = 10$) and bystanders ($n = 8$) were matched for size and weight by tank, and had never met before. Once selected, bystanders and rivals were housed in a square purpose-built tank ($76.2 \times 76.2 \times 25.4$ cm³; Fig. 1). In each of four runs, two bystander fish were placed in the divided centre compartment of the tank, and the five rival fish (A, B, C, D and E) were arranged in units surrounding this central observation unit (Fig. 1). Two pairs of bystanders were trained on $n = 5$ rivals each ($n = 10$ total), and then two more pairs were trained on the same rivals with reversed hierarchy order (see below). Further details are provided in Supplementary Information.

To control for stable physiological differences between fish chosen to be A–E rivals, rival positions were exchanged such that fish serving as the A rival for half of the bystanders served as the E rival for the other half. The same was true for the

B and D rivals. To control for possible spatial effects resulting from consistent location of A next to B and D next to E in the arrangement of rivals around the central bystanders, we also exchanged the spatial locations of the A and E rivals (see Supplementary Information). This spatial exchange was counterbalanced across the position exchange. Together these controls left only fights and transient rival behaviour to influence the bystanders' AE and BD preference, thus controlling for any consistent differences between rival males in physiology, behaviour, or location.

Bystander training on fights between rival males. Bystanders were trained for 7 min per fight and saw two fights a day, one in the morning 2 h after feeding and one 4 h later, for 11 consecutive days (except on days 5, 10 and 11, when bystanders viewed all four possible pairwise fights—see Supplementary Information for complete training details).

At the start of a training trial the rival fish designated to lose was removed from its territory, stressed twice by suspension out of water for 30 s (separated by 1 min) and then placed in the territory of the rival designated to win. The stress, combined with invader status, guaranteed an unambiguous intruder loss. At 1 min after the intruding rival's introduction into the winner's territory, the opaque barrier separating the observer from the competing rivals was removed, and behavioural data were recorded for 7 min. After 7 min the barrier was replaced and the losing rival was returned to its territory, ending the fight.

Bystander preference between novel pairs. Preference during visual presentation of AE and BD pairings was assessed with the use of an approach/avoidance task conducted both in the 'familiar context' (training tank) (bystander choice area: length 45.72 cm, depth 22.86 cm, height 27.94 cm) and in a 'novel context' (unfamiliar tank) specifically designed for testing the approach/avoidance preference in fish¹⁷ (bystander choice area: length 74 cm, depth 37 cm, height 28 cm) (Supplementary Fig. 1). Testing order was counterbalanced, and bystanders were tested on the same pair of rivals in both contexts. Possible effects of test tank differences are discussed in Supplementary Information. During bystander training on pairwise fights suggesting the $A > B > C > D > E$ hierarchy, the order in which bystanders saw B and D lose was counterbalanced to avoid primacy or recency effects; the same was true for A and E (see Supplementary Information).

Each assessment included the following: first, a baseline period, during which the bystander was allowed to swim freely about the tank, but rivals were not visible; second, a forced viewing period during which the bystanders movement was limited to a $4 \times 4 \times 6$ ft³ (1 ft = 0.3048 m) clear plastic box, placed equidistant from visible rival males; and third, a preference period, during which the bystander was allowed to swim freely between the visible rivals. Each period lasted 10 min and scoring was double-blind. T_s was measured between the two farthest quadrants during the preference period, because fish spent nearly all their time in these quadrants when rivals were visible. Further information on preference testing and related controls is provided in Supplementary Information.

Behavioural observations and analysis. *A. burtoni* males have stereotypic patterns of behaviour that reflect their dominance status. In particular, five behavioural variables: chase, bite, flee, lateral threat, and eyebar activation are good indicators of male dominance status^{11–13}. Qualitative ‘winning’ and ‘losing’, as discussed above, were thus defined behaviourally. Losers consistently flee and downregulate their eyebar, whereas winners chase, bite, threaten, and upregulate their own eyebar activation. Overall behavioural differences were quantified with PCA, yielding a DS for each fish in each fight. In all 672 cases, the designated ‘winner’ had a positive DS and the designated ‘loser’ a negative DS. More information on the PCA is provided in Supplementary Information. Permutation *t*-tests and univariate regressions were standard and are discussed in detail in Supplementary Information. *R* was used for plotting and statistical analysis³⁰.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions T.S.C. and L.G. were responsible for experimental design. L.G. was responsible for data collection and analysis. L.G. wrote the manuscript. T.S.C., R.D.F. and L.G. discussed the experiment and edited the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to L.G. (logang@stanford.edu).

CORRIGENDUM

doi:10.1038/nature05642

Genetically modified *Plasmodium* parasites as a protective experimental malaria vaccine

A. K. Mueller, M. Labaied, S. Kappe & K. Matuschewski

Nature 433, 164–176 (2005)

It has been drawn to *Nature's* attention that A.K. M., S. K. and K. M. were named as inventors on a patent application relevant to this work (patent number WO 2005/063991) in 2004, which should therefore have been formally declared as a competing financial interest. The authors' non-profit institutions filed for patent protection to promote the development and distribution of malaria vaccines to people in need worldwide, in accordance with a global access strategy¹.

1. Chen, I. Thinking big about global health. *Cell* 124, 661–663 (2006).

CORRIGENDUM

doi:10.1038/nature05640

Deletion of active ADAMTS5 prevents cartilage degradation in a murine model of osteoarthritis

Sonya S. Glasson, Roger Askew, Barbara Sheppard, Brenda Carito, Tracey Blanchet, Hak-Ling Ma, Carl R. Flannery, Diane Peluso, Kim Kanki, Zhiyong Yang, Manas K. Majumdar & Elisabeth A. Morris

Nature 434, 644–648 (2005)

It has been drawn to *Nature's* attention that E.A.M. and S.S.G. filed a patent application relevant to this work (patent number WO 2006/0004066) under the Patent Cooperation Treaty in 2004, which should therefore have been declared as a competing financial interest.

ERRATUM

doi:10.1038/nature05581

Chronic polyarthritis caused by mammalian DNA that escapes from degradation in macrophages

Kohki Kawane, Mayumi Ohtani, Keiko Miwa, Takuji Kizawa, Yoshiyuki Kanbara, Yoshichika Yoshioka, Hideki Yoshikawa & Shigekazu Nagata

Nature 443, 998–1002 (2006)

In this Letter, the units of the *y*-axis for Fig. 3d should be picograms, not micrograms. The label should read 'TNF- α in serum (pg ml⁻¹)'.

CORRIGENDUM

doi:10.1038/nature05639

A Mesozoic gliding mammal from northeastern China

Jin Meng, Yaoming Hu, Yuanqing Wang, Xiaolin Wang & Chuankui Li

Nature 444, 889–893 (2006)

Of the binomen *Volaticotherium antiquus* established for a Mesozoic gliding mammal discovered from northeastern China, the termination of the trivial name should have a neuter suffix to agree with the gender of the generic name¹. The species name is therefore corrected to *Volaticotherium antiquum*.

1. International Commission on Zoological Nomenclature. *International Code of Zoological Nomenclature* 4th edn (International Trust for Zoological Nomenclature, The Natural History Museum, London, 1999).

ERRATUM

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Fish can infer social rank by observation alone

Logan Grosenick, Tricia S. Clement & Russell D. Fernald

Nature 445, 429–432 (2007)

In the print version of this Letter, the significance level for hypothesis testing was incorrect for the 'first-choice' results (line 19 on page 430) and should be 0.05 instead of 0.01. The online PDF and HTML versions are correct.

ADDENDUM

doi:10.1038/nature05607

Artificial 'spin ice' in a geometrically frustrated lattice of nanoscale ferromagnetic islands

R. F. Wang, C. Nisoli, R. S. Freitas, J. Li, W. McConville, B. J. Cooley, M. S. Lund, N. Samarth, C. Leighton, V. H. Crespi & P. Schiffer

Nature 439, 303–306 (2006)

During the field treatment of the samples prior to measurement, the magnetic field was switched in polarity with each step down in magnitude while the sample was being rotated within the magnetic field. A more detailed description of the field treatment can be found in ref. 1.

1. Wang, R. F. *et al.* Demagnetization protocols for frustrated interacting nanomagnet arrays. *J. Appl. Phys.* (in the press); preprint at (<http://arxiv.org/abs/cond-mat/0702084>) (2007).