

the decrease in resistance because of an increase of current in the path with the higher current.

The induction of a conducting path in the absence of light is clearly triggered by the presence of the first path, because at constant temperature  $V_{ind}$  decreases with higher current flow through the conducting path and with closer proximity to the first path. The distance across which a metallic path can be induced can be much greater than the distance at which a change of reflectivity due to the formation of metallic patches can be detected. The trigger voltage is distinctly dependent on temperature, whereas the width of a conducting path is not.

The successful visualization of the local photoinduced I-M transition by the depicted differential reflection technique opens the way for a variety of further experimental studies. Our observations already indicate that the requirements for creating the transition and maintaining the transition are fundamentally different. With respect to applications, the local I-M transition is a tool for switching the resistivity of a material by many orders of magnitude in a controllable and observable way. The generation and removal of one or more conducting paths at arbitrarily chosen spots of a sample is performed by the appropriate choice of external parameters and monitored with visible light. These features suggest an application of the local photoinduced I-M transition in the construction of optical switching devices. In the experiment, a gap of 150  $\mu\text{m}$  between the electrodes was chosen to simplify the imaging, and a regulated dc power supply was used for experimental convenience. With a gap width of 25  $\mu\text{m}$ , however, the applied voltage could be reduced to the order of 1 V, which can be provided by ordinary power supplies.

## REFERENCES AND NOTES

1. A. J. Millis, *Nature* **392**, 147 (1998).
2. Z. Jirak, S. Krupicka, Z. Simsa, M. Dlouha, S. Vratislav, *J. Magn. Magn. Mater.* **53**, 153 (1985).
3. Y. Tomioka, A. Asamitsu, H. Kuwahara, Y. Morimoto, Y. Tokura, *Phys. Rev. B* **53**, R1689 (1996).
4. H. Yoshisawa, H. Kawano, Y. Tokura, *ibid.* **52**, 13145 (1995).
5. A. Asamitsu, Y. Tomioka, H. Kuwahara, Y. Tokura, *Nature* **388**, 50 (1997).
6. Y. Morimoto, H. Kuwahara, Y. Tomioka, Y. Tokura, *Phys. Rev. B* **55**, 7549 (1997).
7. V. Kiryukhin *et al.*, *Nature* **386**, 813 (1997).
8. K. Miyano, T. Tanaka, Y. Tomioka, Y. Tokura, *Phys. Rev. Lett.* **78**, 4257 (1997).
9. W. Eberle *et al.*, *Appl. Phys. Lett.* **68**, 3329 (1996).
10. W. Prettl, in *Nonlinear Physics of Complex Systems. Current Status and Future Trends*, J. Parisi, S. C. Müller, W. Zimmermann, Eds. (Springer-Verlag, Berlin, 1996), pp. 341–352.
11. N. Balkan, B. K. Ridley, A. J. Vickers, Eds., *Negative Differential Resistance and Instabilities in 2D Semiconductors*, NATO Advanced Research Workshop, Il Ciocco, Lucca, Italy (NATO ASI Series, Overijse, Netherlands, 1992).
12. Y. Tomioka, A. Asamitsu, Y. Morimoto, Y. Tokura, J.

- Phys. Soc. Jpn.* **64**, 3626 (1995).
13. T. Mori *et al.*, *ibid.* **66**, 3570 (1997).
14. K. Ogawa, W. Wei, K. Miyano, Y. Tomioka, Y. Tokura, *Phys. Rev. B*, in press.
15. Y. Okimoto, Y. Tomioka, Y. Onose, Y. Otsuka, Y. Tokura, *Phys. Rev. B*, in press.
16. Supported in part by the Core Research for Evolu-

tional Science and Technology (CREST) of JST, and by a Grant-in-Aid for Center of Excellence Research from the Ministry of Education, Science, Sports and Culture of Japan. The work at JRCAT was supported by The New Energy and Industrial Technology Development Organization.

5 March 1998; accepted 7 May 1998

## Call Duration as an Indicator of Genetic Quality in Male Gray Tree Frogs

Allison M. Welch,\* Raymond D. Semlitsch, H. Carl Gerhardt

The “good genes” hypothesis predicts that mating preferences enable females to select mates of superior genetic quality. The genetic consequences of the preference shown by female gray tree frogs for long-duration calls were evaluated by comparing the performance of maternal half-siblings sired by males with different call durations. Offspring of male gray tree frogs that produced long calls showed better performance during larval and juvenile stages than did offspring of males that produced short calls. These data suggest that call duration can function as a reliable indicator of heritable genetic quality.

The “good genes” model of sexual selection predicts that some attributes of male courtship displays advertise genetic quality. Preferences for such attributes should allow females to mate with high-quality males and thereby benefit indirectly through enhanced quality of offspring (1). Although the good genes hypothesis has been tested several times (2), few studies have provided direct genetic evidence supporting this hypothesis (3). Only one such study involved a species in which females cannot benefit directly from their choice of mates (4). Because selection for direct benefits such as courtship feeding or parental care should overwhelm any selection for indirect (genetic) benefits (5), the role of good genes selection in the evolution and maintenance of female preferences is best tested in species in which females do not benefit directly from mate choice.

Female gray tree frogs (*Hyla versicolor*) strongly prefer male advertisement calls of long duration in laboratory experiments (6, 7). In the field, females freely initiate matings with calling males and do not always choose the first male encountered (7). Because males do not defend oviposition sites, offer nuptial gifts, or contribute parental care (8, 9), and no difference has been found in fertilization success as a function of call duration (10), there are no apparent direct benefits of a female's mate choice. We therefore predicted that females selecting mates with long calls should benefit indirectly

through increased fitness of offspring. This prediction can be tested by evaluating the relation between paternal call duration and the genetic quality of offspring.

Male gray tree frog advertisement calls consist of rapidly repeated pulses. In dense choruses and in response to playbacks, males tend to increase call duration by increasing the number of pulses per call (11, 12). Nonetheless, some males consistently produce longer calls than others in the same acoustic environment (7, 12–14). Although long calls are usually produced at slow rates, thereby keeping aerobic metabolic costs relatively constant (11, 14), males that produce long calls spend less time calling per night (11) and attend fewer choruses per season (8) than males that produce short calls. Long calls thus appear to impose higher nonaerobic costs than short calls. Call duration may, therefore, be an honest indicator of male genetic quality.

We tested whether call duration indicates heritable genetic quality by using maternal half-siblingships (half-sibships) to compare the performance of different males' offspring while experimentally controlling for all maternal effects. Maternal half-sibships were generated by artificially crossing each female with two males that had been giving calls of distinctly different durations in the same social environment (Table 1). Thus, within each maternal half-sibship, one sibship was sired by a male with calls of longer duration than the male siring the other sibship. Because call duration varies with chorus density, males' calls must be assessed in the same social context in order to be validly compared. Thus, in 1995 we selected nine sets of two males that had

Division of Biological Sciences, University of Missouri, Columbia, MO 65211, USA.

\*To whom correspondence should be addressed. E-mail: awelch@biosci.mbp.missouri.edu

been calling within 2 m of each other, and in 1996 we selected six sets of two field-caught males that had been calling simultaneously in a small captive chorus. The mean difference in call duration between the long- and the short-caller in each set was 10.1 pulses per call in 1995 and 15.8 pulses per call in 1996 (Table 1); in laboratory experiments, female *H. versicolor* routinely base preferences on differences of as few as 2 pulses per call (15). Furthermore, the average call durations of individual males classified as long-callers did not overlap with the average call durations of individuals classified as short-callers (16). Long- and short-callers did not differ in body mass. External artificial fertilization allowed unambiguous assignment of paternity, and rotation of the egg-stripping of each female between the pair of males eliminated the possibility of effects of fertilization order (17). In 1995, each of nine gravid females was artificially crossed with a different set of males to generate nine maternal half-sibships. In 1996, each of 11 gravid females was artificially crossed with at least one set of males to generate 16 maternal half-sibships. All frogs were collected near a pond in Boone County,

Missouri.

Because the relative performance of different genotypes can vary significantly with environmental conditions (18), we reared the resulting tadpoles at two food levels, thereby creating an unfavorable and a favorable growth environment in which to compare the performance of offspring (19). Comparison of our results with those from field studies indicates that our high food treatment was a realistic approximation of conditions encountered in nature (20). Tadpoles from the crosses (1995,  $n = 538$ ; 1996,  $n = 384$ ) were raised individually in containers filled with 1.0 liter of water in the laboratory at the two food levels; 15 tadpoles per family were reared at each food level in 1995 and six tadpoles per family in 1996 (21). To assess offspring performance, we used several variables (22) that are important determinants of fitness in anurans, predicting future survival and age and size at maturity, which influence lifetime reproductive success (23).

Offspring of males with long calls always performed significantly better than or not significantly differently from offspring of males with short calls (24) (Table 2). In multivariate analyses where responses were combined to account for correlations

among response variables (25), the main effect of call duration was significant at both food levels in 1996 and showed the same trend at both food levels in 1995 (Table 2), with offspring of males with long calls showing a general performance advantage over offspring of males with short calls. The probability of obtaining these four multivariate results that independently support the same directional hypothesis was calculated as  $P = 0.0008$  (Table 2) with the use of a combined probability test (26). The multivariate tests therefore support the hypothesis that offspring performance is predicted by paternal call duration.

The specific benefits realized by offspring of long-callers differed among our experimental environments (Table 2). Because variation in the quality of the growth environment is predicted to influence the relation between larval growth and development (27), this difference in responses among environments is not unexpected. The consistency of the general benefit realized by offspring of long-callers in our experimental environments suggests that a general performance advantage may be applicable in other environments as well.

Overall, these results provide strong evidence that males with long calls relative to those of other males in the same social environment sired offspring of significantly higher phenotypic quality than males with short relative call durations. We can attribute these observed phenotypic differences to differences in paternal genetic contribution, because our comparison of maternal half-sibships controls for maternal genetic contributions and maternal effects. Thus, our results demonstrate that relative call duration reliably reflects genetic quality in *H. versicolor*. Our data suggest a genetic correlation between sire call duration and offspring performance, which implies that each trait has a heritable basis. The preference for long calls should, therefore, enable females to select high-quality mates and benefit indirectly through increased fitness of offspring. Because female *H. versicolor* do not gain direct benefits from their choice of mate, the indirect genetic benefits we have documented suggest good genes selection as a probable explanation for the evolution and maintenance of the female preference in this species.

## REFERENCES AND NOTES

1. A. Zahavi, *J. Theor. Biol.* **53**, 205 (1975).
2. R. D. Howard, H. H. Whiteman, T. I. Schueller, *Evolution* **48**, 1286 (1994); R. D. Semlitsch, *Behav. Ecol. Sociobiol.* **34**, 19 (1994); B. D. Woodward, *Am. Nat.* **128**, 58 (1986); S. L. Mitchell, *Evolution* **44**, 502 (1990).
3. K. Norris, *Nature* **362**, 537 (1993); B. C. Sheldon, J. Merilä, A. Qvarnström, L. Gustafsson, H. Ellegren,

**Table 1.** Average calling performance of sires exhibiting long versus short calls. For each 1995 male, approximately 25 consecutive calls were analyzed from field recordings. For each 1996 male, at least 20 min of consecutive calls were analyzed from digitally collected data.

Year	Performance	Call duration		Calling effort*
		Pulses per call	Seconds	
1995	Long-callers	28.3	1.74	0.214
	Short-callers	18.2	1.05	0.188
	Difference	$10.1 \pm 4.9^\dagger$	$0.69 \pm 0.36^\dagger$	$0.026 \pm 0.040^\ddagger$
1996	Long-callers	31.5	1.41	0.092
	Short-callers	15.7	0.68	0.082
	Difference	$15.8 \pm 4.6^\dagger$	$0.72 \pm 0.24^\dagger$	$0.010 \pm 0.048^\ddagger$

\*Calling effort was measured as duty cycle—the proportion of time during which the individual was producing sound.  $^\dagger P < 0.001$ ; paired  $t$  test.  $^\ddagger P > 0.05$ ; paired  $t$  test.

**Table 2.** Relative performance of offspring of males exhibiting long versus short calls. A shorter larval period is interpreted as better performance. For all other variables, larger values indicate better performance. NS, not significant. Dashes indicate data not collected in 1995.

Parameter	1995		1996	
	High food	Low food	High food	Low food
Larval growth	NS*	Long $\gg$ short $^\dagger$	Long $\gg$ short	Long $>$ short $^\ddagger$
Larval period	Long $\gg$ short	NS	Long $\gg$ short	NS
Metamorphic mass	NS	Long $>$ short	NS	NS
Larval survival	Long $>$ short	NS	NS	NS
Postmetamorphic growth	—	—	NS	Long $\gg$ short
MANOVA	$\lambda = 0.96$ , df = 3, $P = 0.0887$	$\lambda = 0.81$ , df = 3, $P = 0.0590$	$\lambda = 0.90$ , df = 4, $P = 0.0143$	$\lambda = 0.71$ , df = 4, $P = 0.0216$
Combined probability test	$\chi^2 = 26.67$ , df = 8, $P = 0.0008$			

\*NS =  $P > 0.05$ ; univariate ANOVA (24).  $^\dagger$ Long  $\gg$  short =  $P < 0.01$ .  $^\ddagger$ Long  $>$  short =  $0.05 > P > 0.01$ .

- Proc. R. Soc. London Ser. B* **264**, 297 (1997).
4. M. Petrie, *Nature* **371**, 598 (1994).
  5. M. Kirkpatrick and N. H. Barton *Proc. Natl. Acad. Sci. U.S.A.* **94**, 1282 (1997).
  6. G. M. Klump and H. C. Gerhardt, *Nature* **326**, 286 (1987).
  7. H. C. Gerhardt, M. L. Dyson, S. D. Tanner, *Behav. Ecol. 7*, 7 (1996).
  8. B. K. Sullivan and S. H. Hinshaw, *Anim. Behav.* **44**, 733 (1992).
  9. G. M. Fellers, *Copeia* **1979**, 286 (1979).
  10. J. D. Krenz, unpublished data.
  11. K. D. Wells and T. L. Taigen, *Behav. Ecol. Sociobiol.* **19**, 9 (1986).
  12. H. C. Gerhardt, *Anim. Behav.* **42**, 615 (1991).
  13. L. S. Runkle, K. D. Wells, C. C. Robb, S. L. Lance, *Behav. Ecol.* **5**, 318 (1994).
  14. U. Grafe, *Copeia* **1997**, 356 (1997).
  15. H. C. Gerhardt and G. F. Watson, *Anim. Behav.* **50**, 1187 (1995); H. C. Gerhardt and S. D. Tanner, unpublished data.
  16. In 1995, average numbers of pulses per call ranged from 15.3 to 21.8 for individual short-callers and from 22.1 to 38.7 for long-callers. In 1996, average pulse numbers ranged from 14.4 to 18.0 for short-callers and from 22.1 to 37.7 for long-callers.
  17. R. D. Semlitsch, S. Schmiedehausen, H. Hotz, P. Beerli, *Evol. Ecol.* **10**, 531 (1996); R. D. Semlitsch, H. Hotz, G.-D. Guex, *Evolution* **51**, 1249 (1997).
  18. D. S. Falconer and T. F. C. Mackay, *Introduction to Quantitative Genetics* (Longman, Essex, ed. 4, 1996).
  19. Tadpoles were fed finely ground Tetra-Min fish flakes. The high food ration was typically as much as the tadpoles could consume and was always three times the low food ration. Larval survival, growth rate, length of larval period, and mass at metamorphosis differed significantly between the two food levels in both years ( $P < 0.001$ ,  $t$  tests), demonstrating that the low food level constituted a significantly less favorable environment than the high food level.
  20. Individuals metamorphosing from our high food treatment weighed an average of 0.359 g in 1995 and 0.319 g in 1996. Average mass at metamorphosis of *H. versicolor* reared in field enclosures was 0.340 g in the sun and 0.310 g in the shade (13). In a natural population of *H. chrysoscelis* (the cryptic sister species of *H. versicolor*), average mass at metamorphosis was 0.33 g (28).
  21. Tadpoles were randomly assigned to food levels and blocks within our randomized block design. The experiment was conducted blind with respect to genetic identity.
  22. Performance was measured as follows: wet mass (to the nearest milligram) on day 30 of the experiment—a measure of early larval growth rate; the larval period in days from the beginning of the experiment (stage 25) (29) to forelimb emergence (stage 42); and wet mass (to the nearest milligram) of metamorphs after tail resorption (stage 46). Larval survival was calculated as the proportion of individuals from each family surviving to metamorphosis. In 1996, postmetamorphic growth was calculated as the difference between wet mass achieved 30 days after metamorphosis and wet mass at metamorphosis.
  23. K. A. Berven and D. E. Gill, *Am. Zool.* **23**, 85 (1983); D. C. Smith, *Ecology* **68**, 344 (1987).
  24. Mixed-model univariate analyses of variance (ANOVAs) were performed for each response variable, at each food level during each year, to test for the main effects of call duration, maternal identity, paternal identity (1996 only), and blocking factors, as well as for interactions. In order to account for correlations between larval period and metamorphic mass, each was used as a covariate in the univariate analyses of the other. Metamorphic mass was also used as a covariate in analyses of postmetamorphic growth. ANOVA tables and more complete descriptions of analyses can be found at [www.sciencemag.org/feature/data/976682.shl](http://www.sciencemag.org/feature/data/976682.shl).
  25. A multivariate analysis of variance (MANOVA) was used for each food level during each year to test for multivariate effects of call duration, maternal identity, paternal identity (1996 only), and blocking factors. MANOVAs simultaneously included larval growth, larval period, metamorphic mass, and (in 1996) post-metamorphic growth but did not include survival because the unit of analysis for this variable was the family rather than the individual. We present results for the multivariate effect of call duration, based on Wilks'  $\lambda$ . Data were appropriately transformed in both univariate and multivariate analyses.
  26. R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1981).
  27. H. M. Wilbur and J. P. Collins, *Science* **182**, 1305 (1973); J. Travis, *Evolution* **44**, 502 (1984).
  28. M. E. Ritke, J. G. Babb, M. K. Ritke, *J. Herpetol.* **24**, 135 (1990).
  29. K. L. Gosner, *Herpetologica* **16**, 183 (1960).
  30. We thank B. Buchanan and J. Schwartz for help in assessing males in 1996; J. Krenz for help with artificial crosses in 1996; A. Bullerdieck for assistance in raising tadpoles in 1996; M. Cherry, M. Cunningham, J. Krenz, M. Parris, A. Pomiankowski, T. Ryan, and J. Schwartz for comments on the manuscript; and the many people who helped collect frogs. This work was supported by an NSF predoctoral fellowship (A.M.W.), NSF and NIMH grants (H.C.G.), and a Sigma Xi Grant-in-aid of Research (A.M.W.).

12 December 1997; accepted 22 April 1998

## Neural Correlates of Perceptual Rivalry in the Human Brain

Erik D. Lumer,\* Karl J. Friston, Geraint Rees

When dissimilar images are presented to the two eyes, perception alternates spontaneously between each monocular view, a phenomenon called binocular rivalry. Functional brain imaging in humans was used to study the neural basis of these subjective perceptual changes. Cortical regions whose activity reflected perceptual transitions included extrastriate areas of the ventral visual pathway, and parietal and frontal regions that have been implicated in spatial attention; whereas the extrastriate areas were also engaged by nonrivalrous perceptual changes, activity in the frontoparietal cortex was specifically associated with perceptual alternation only during rivalry. These results suggest that frontoparietal areas play a central role in conscious perception, biasing the content of visual awareness toward abstract internal representations of visual scenes, rather than simply toward space.

Binocular rivalry provides a useful experimental paradigm with which to study the neural correlates of conscious perception (1–3). When dissimilar images are presented to the two eyes, they compete for perceptual dominance so that each image is visible in turn for a few seconds while the other is suppressed. Because perceptual transitions between each monocular view occur spontaneously without any change in the physical stimulus, neural responses associated with perceptual processes can be distinguished from those due to stimulus characteristics. Recent neurophysiological studies in awake monkeys have established that, whereas the firing of most neurons in primary visual cortex (V1) correlates with the stimulus and not the percept during rivalry, activity of neurons at higher levels in the visual pathway, such as in the inferotemporal cortex, reflects the perceptual state (3). These findings suggest that rivalry results from a competition between alternative stimulus interpretations at a level beyond the stages of monocular processing early in visual cortex (4). Psychophysical observations also suggest that perceptual alternation during rivalry results from the same neural operations underlying other multi-

stable perceptual phenomena, such as depth reversals and ambiguous figures, that show similar temporal dynamics to binocular rivalry (5). Although less pronounced, similar perceptual fluctuations can also be experienced in normal vision and may therefore reflect a basic perceptual strategy to resolve visual ambiguity (6). Yet despite significant interest in the neural correlates of binocular rivalry (1–3), the mechanisms underlying these perceptual alternations remain unknown.

Here we investigate these mechanisms by characterizing neural activity associated with perceptual transitions per se, rather than activity associated with perceptual state during rivalry. Our results provide evidence for an involvement not only of occipitotemporal visual areas in binocular rivalry, but also indicate a specific and previously unknown role for frontoparietal areas in mediating the perceptual transitions experienced during rivalry. These results were obtained by measuring brain activity with functional magnetic resonance imaging (fMRI) in humans who reported their percepts under two different viewing conditions (7). In the first condition, subjects viewed dichoptic stimuli consisting of a red-colored drifting grating shown to one eye and a green-colored face shown to the other eye. These images were chosen because they are highly dissimilar and readily produce full-field rivalry when

Wellcome Department of Cognitive Neurology, Institute of Neurology, University College London, Queen Square, London WC1N 3BG, UK.

\*To whom correspondence should be addressed. E-mail: [elumer@fil.ion.ucl.ac.uk](mailto:elumer@fil.ion.ucl.ac.uk)