Call Duration as an Indicator of Genetic Quality in Male Gray Tree Frogs
Allison M. Welch et al.
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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 $V_{\text{bias}}$ 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 $\mu$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 $\mu$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**

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**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 relationship 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-sibships (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
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 individual 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 allowed unambiguous assignment of paternal males classified as long-callers did not differ in paternal genetic contributions and 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.

### 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.

<table>
<thead>
<tr>
<th>Year</th>
<th>Performance</th>
<th>Call duration</th>
<th>Calling effort*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Pulses per call</td>
<td>Seconds</td>
</tr>
<tr>
<td>1995</td>
<td>Long-callers</td>
<td>28.3</td>
<td>1.74</td>
</tr>
<tr>
<td></td>
<td>Short-callers</td>
<td>18.2</td>
<td>1.05</td>
</tr>
<tr>
<td>1996</td>
<td>Long-callers</td>
<td>31.5</td>
<td>1.41</td>
</tr>
<tr>
<td></td>
<td>Short-callers</td>
<td>15.7</td>
<td>0.68</td>
</tr>
</tbody>
</table>

- Calling effort was measured as duty cycle—the proportion of time during which the individual was producing sound. †P < 0.001; paired t test. ‡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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>1995</th>
<th>1996</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High food</td>
<td>Low food</td>
</tr>
<tr>
<td>Larval growth</td>
<td>NS*</td>
<td>Long &gt;</td>
</tr>
<tr>
<td>Larval period</td>
<td>Long &gt;</td>
<td>short</td>
</tr>
<tr>
<td>Metamorphic mass</td>
<td>NS</td>
<td>Long &gt;</td>
</tr>
<tr>
<td>Larval survival</td>
<td>Long &gt;</td>
<td>short</td>
</tr>
<tr>
<td>Postmetamorphic</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>growth MANOVA</td>
<td>( \lambda = 0.96, df = 3, )</td>
<td>( \lambda = 0.81, df = 3, )</td>
</tr>
<tr>
<td>Combined probability</td>
<td>( \chi^2 = 26.67, df = 8, P = 0.0008 )</td>
<td></td>
</tr>
</tbody>
</table>

*NS = P > 0.05; univariate ANOVA (24). †Long > short: \( P < 0.01 \). ‡Long > short: \( 0.05 > P > 0.01 \).

### REFERENCES AND NOTES

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, parietal and frontal regions that have been implicated in spatial attention; whereas the extrastriate areas were also engaged by nonvisual 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 an external cue, 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 other neural processes underlying other multidimensional 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 dichotic 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...