

system of the Lake Michigan mottled sculpin, Cottus bairdi Hydrodynamic image formation by the peripheral lateral line

Sheryl Coombs, James J. Finneran and Ruth A. Conley

doi: 10.1098/rstb.2000.0649 Phil. Trans. R. Soc. Lond. B 2000 **355**, 1111-1114

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 **Hydrodynamic image formation by the peripheral lateral line system of the Lake

Michigan mattled soulpin Cettus boirding Hydrodynamic image formation by the eripheral lateral line system of the Lake Michigan mottled sculpin, Cottus bairdi**

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19 *Alexander Chicago, 6525 North Sheridan Road, Chicago*
2²SPAWAR Systems Center, San Diego, CA 92152-6505, USA
28 Actor Chicago Readley University Peoria II 61625, USA itute, Loyola University of Chicago, 6525 North Sheridan Road, Chicago, .
²SPAWAR Systems Center, San Diego, CA 92152-6505, USA
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Lake Michigan mottled sculpin (*Cottus bairdi*) have a lateral-line-mediated prey-capture behaviour that

Lake Michigan mottled sculpin *(Cottus bairdi)* have a lateral-line-mediated prey-capture behaviour that consists of an initial orientation towards the prey, a sequence of approach movements, and a final strike at the prey Lake Michigan mottled sculpin *(Cottus bairdi)* have a lateral-line-mediated prey-capture behaviour that consists of an initial orientation towards the prey, a sequence of approach movements, and a final strike at the prey consists of an initial orientation towards the prey, a sequence of approach movements, and a final strike at
the prey. This unconditioned behaviour can be elicited from blinded sculpin in the laboratory by both
real and ar the prey. This unconditioned behaviour can be elicited from blinded sculpin in the laboratory by both
real and artificial (vibrating sphere) prey. In order to visualize what Lake Michigan mottled sculpin
might perceive thr real and artificial (vibrating sphere) prey. In order to visualize what Lake Michigan mottled sculpin
might perceive through their lateral line when approaching prey, we have combined anatomical, neuro-
physiological, beha might perceive through their lateral line when approaching prey, we have combined anatomical, neuro-
physiological, behavioural and computational modelling techniques to produce three-dimensional maps
of how excitation pat physiological, behavioural and computational modelling techniques to produce three-dimensional maps
of how excitation patterns along the lateral line sensory surface change as sculpin approach a vibrating
sphere. Changes i of how excitation patterns along the lateral line sensory surface change as sculpin approach a vibrating sphere. Changes in the excitation patterns and the information they contain about source location are consistent with sphere. Changes in the excitation patterns and the information they contain about source location are consistent with behavioural performance, including the approach pathways taken by sculpin to the sphere, the maximum dis consistent with behavioural performance, including the approach pathways taken by sculpin to the sphere, the maximum distances at which approaches can be elicited, distances from which strikes are launched, and strike succ sphere, the maximum distances at which approaches can be elicited, distances from which strikes are launched, and strike success. Information content is generally higher for laterally located sources than for frontally loc launched, and strike success. Information content is generally higher for laterally located sources than for
frontally located sources and this may explain exceptional performance (e.g. successful strikes from
unusually lo frontally located sc
unusually long dista
to frontal sources. unusually long distances) in response to lateral sources and poor performance (e.g. unsuccessful strikes) to frontal sources.
 Keywords: lateral line; localization; feeding behaviour; prey detection

1. INTRODUCTION

1. INTRODUCTION
The lateral line system is one of the most primitive, but
perhaps least understood of all vertebrate sensory systems **PERTUANCE TON**
The lateral line system is one of the most primitive, but
perhaps least understood of all vertebrate sensory systems,
especially given that its general function as a water-The lateral line system is one of the most primitive, but
perhaps least understood of all vertebrate sensory systems,
especially given that its general function as a water-
current detector has been known for close to a ce perhaps least understood of all vertebrate sensory systems,
especially given that its general function as a water-
current detector has been known for close to a century
(Hofer 1908). One of the biggest impediments to unde especially given that its general function as a water-
current detector has been known for close to a century
(Hofer 1908). One of the biggest impediments to under-
standing how this spatially distributed system works is t current detector has been known for close to a century
(Hofer 1908). One of the biggest impediments to under-
standing how this spatially distributed system works is the
inherent difficulty in adequately specifying and (Hofer 1908). One of the biggest impediments to understanding how this spatially distributed system works is the inherent difficulty in adequately specifying and measuring hydrodynamic stimuli which can vary in inherent difficulty in adequately specifying and
measuring hydrodynamic stimuli, which can vary in
frequency, amplitude and phase along the sensory surface
of the animal Even the simplest of sources—a sinusoidmeasuring hydrodynamic stimuli, which can vary in
frequency, amplitude and phase along the sensory surface
of the animal. Even the simplest of sources—a sinusoid-
ally vibrating sphere for example—can produce a rather frequency, amplitude and phase along the sensory surface
of the animal. Even the simplest of sources—a sinusoid-
ally vibrating sphere, for example—can produce a rather
complex stimulus field. Eurthermore, the peripheral e of the animal. Even the simplest of sources—a sinusoidally vibrating sphere, for example—can produce a rather complex stimulus field. Furthermore, the peripheral excially vibrating sphere, for example—can produce a rather
complex stimulus field. Furthermore, the peripheral exci-
tation pattern that results after the stimulus field has been
transduced can be even more complex and depend complex stimulus field. Furthermore, the peripheral excitation pattern that results after the stimulus field has been
transduced can be even more complex and depends on a
number of factors, including the number, type and s tation pattern that results after the stimulus field has been
transduced can be even more complex and depends on a
number of factors, including the number, type and spatial
distribution of lateral line end organs on the fi transduced can be even more complex and depends on a
number of factors, including the number, type and spatial
distribution of lateral line end organs on the fish, the axis
of source vibration, and the distance and orienta number of factors, including the number, type and spatial
distribution of lateral line end organs on the fish, the axis
of source vibration, and the distance and orientation of
the fish with respect to the source (Denton & distribution of lateral line end organs on the fish, the axis
of source vibration, and the distance and orientation of
the fish with respect to the source (Denton & Gray 1983;
Coombs *et al* 1996) of source vibration, and the distance and orientation of the fish with respect to the source (Denton & Gray 1983; Coombs *et al.* 1996). E fish with respect to the source (Denton & Gray 1983;
bombs *et al.* 1996).
For the last few years, we have been interested in the
estion of what fish actually perceive through their

Coombs *et al.* 1996).

For the last few years, we have been interested in the question of what fish actually perceive through their

lateral line system. Although it may prove impossible to For the last few years, we have been interested in the question of what fish actually perceive through their lateral line system. Although it may prove impossible to determine the ultimate percent we can model 'hydroquestion of what fish actually perceive through their
lateral line system. Although it may prove impossible to
determine the ultimate percept, we can model 'hydrodynamic images' at the level of the peripheral nervous

standing how this spatially distributed system works is the field is represented in the activity of peripheral nerve
inherent difficulty in adequately specifying and fibres innervating different end organs at different loc system and use these models to determine how information about stimulus sources (e.g. location, size, shape, etc.) might be conveyed to the central nervous system. Towards tion about stimulus sources (e.g. location, size, shape, etc.)
might be conveyed to the central nervous system. Towards
that end, we have used a combination of anatomical,
physiological behavioural and computational approa might be conveyed to the central nervous system. Towards
that end, we have used a combination of anatomical,
physiological, behavioural and computational approaches
to determine (i) the three-dimensional stimulus field that end, we have used a combination of anatomical,
physiological, behavioural and computational approaches
to determine (i) the three-dimensional stimulus field
about a dinole source (vibrating sphere): (ii) how this physiological, behavioural and computational approaches
to determine (i) the three-dimensional stimulus field
about a dipole source (vibrating sphere); (ii) how this
field is represented in the activity of peripheral nerve to determine (i) the three-dimensional stimulus field
about a dipole source (vibrating sphere); (ii) how this
field is represented in the activity of peripheral nerve
fibres innervating different end organs at different lo about a dipole source (vibrating sphere); (ii) how this
field is represented in the activity of peripheral nerve
fibres innervating different end organs at different loca-
tions within the field: and (iii) how excitation p field is represented in the activity of peripheral nerve fibres innervating different end organs at different locations within the field; and (iii) how excitation patterns across fibres change as fish approach dipole sources in the hiologically relevant context of feeding behavi tions within the field; and (iii) how excitation patterns
across fibres change as fish approach dipole sources in the
biologically relevant context of feeding behaviour
(Coombs et al. 1996: Coombs & Conley 1997a b: Conley across fibres change as fish approach dipole sources in the
biologically relevant context of feeding behaviour
(Coombs *et al.* 1996; Coombs & Conley 1997*a,b*; Conley
& Coombs 1998) The purpose of this paper is to review biologically relevant context of feeding behaviour (Coombs *et al.* 1996; Coombs & Conley 1997*a,b*; Conley & Coombs 1998). The purpose of this paper is to review briefly this multi-dimensional approach and its under-(Coombs *et al.* 1996; Coombs & Conley 1997*a,b*; Conley & Coombs 1998). The purpose of this paper is to review briefly this multi-dimensional approach and its under-
lying assumptions to summarize some of the key finding & Coombs 1998). The purpose of this paper is to review
briefly this multi-dimensional approach and its under-
lying assumptions, to summarize some of the key findings
and testable predictions arising from this approach and lying assumptions, to summarize some of the key findings and testable predictions arising from this approach, and lying assumptions, to summarize some of the key findings
and testable predictions arising from this approach, and
to report some new modelling results, using the latest
iteration of our computational model to provide an an and testable predictions arising from this approach, and
to report some new modelling results, using the latest
iteration of our computational model to provide an anato-
mically correct, three-dimensional model of excitati to report some new modelling results, using the latest
iteration of our computational model to provide an anato-
mically correct, three-dimensional model of excitation
patterns over the entire lateral line sensory surface iteration of our computational model to provide an anato-
mically correct, three-dimensional model of excitation
patterns over the entire lateral line sensory surface of the fish. tterns over the entire lateral line sensory surface of the
h.
One of the keys to the success of this overall strategy is
a prev-capture behaviour of Lake Michigan mottled

fish.
One of the keys to the success of this overall strategy is
the prey-capture behaviour of Lake Michigan mottled
sculpin (Cattus hairdi). After responding with an initial One of the keys to the success of this overall strategy is
the prey-capture behaviour of Lake Michigan mottled
sculpin *(Cottus bairdi*). After responding with an initial
orientating response at the time of prey detection the prey-capture behaviour of Lake Michigan mottled
sculpin *(Cottus bairdi)*. After responding with an initial
orientating response at the time of prey detection, these
benthic sculpin approach their prey along the substr sculpin *(Cottus bairdi)*. After responding with an initial orientating response at the time of prey detection, these benthic sculpin approach their prey along the substrate in a saltatory fashion stopping for several seco orientating response at the time of prey detection, these benthic sculpin approach their prey along the substrate in a saltatory fashion, stopping for several seconds after each

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Figure 1. Lateral line excitation patterns as a function of source distance (*a*) and source size (*b*). In (*a*), excitation patterns are modelled along a theoretical linear array of source distance (*a*) and source size (*b*). In (*a*), excitation patterns are modelled along a theoretical linear array of lateral line canal neuromasts spanning the length (100 mm) of a mottled sculpin from head to tail. The array is placed at of a mottled sculpin from head to tail. The array is placed at 10, 20, 40, 60, 80, 100, and 120 mm away from a 50 Hz dipole source, 6 mm in diameter and with a 1 m s^{-1} source velocity. The arrow indicates the axis of 10, 20, 40, 60, 80, 100, and 120 mm away from a 50 Hz dipole source, 6 mm in diameter and with a 1 m s^{-1} source
velocity. The arrow indicates the axis of source vibration.
In (b) , the excitation pattern is modelled for a source of the
same frequency and velocity, but f **SCIENCES** velocity. The arrow indicates the axis of source vibration.
In (b) , the excitation pattern is modelled for a source of the same frequency and velocity, but four times the diameter at In (b) , the excitation pattern is modelled for a source of the same frequency and velocity, but four times the diameter at a distance of 40 mm. In both (a) and (b) , local accelerations (pressure-difference amplitudes) same frequency and velocity, but four times the diameter at
a distance of 40 mm. In both (a) and (b) , local accelerations
(pressure-difference amplitudes) of the surrounding water
were computed over 2 mm intervals, the (pressure-difference amplitudes) of the surrounding water
were computed over 2 mm intervals, the average interpore were computed over 2 mm intervals, the average interpore
spacing on the trunk canal of the mottled sculpin. Pressure-
difference directions along the long axis of the canal are
represented by opposite ends of the spectrum, spacing on the trunk canal of the mottled sculpin. Pressurespacing on the trunk canal of the mottled sculpin. Pressure-
difference directions along the long axis of the canal are
represented by opposite ends of the spectrum, with positive
pressure differences (flow in one directio difference directions along the long axis of the canal are
represented by opposite ends of the spectrum, with positive
pressure differences (flow in one direction) at the red end of
the spectrum and negative differences (f represented by opposite ends of the spectrum, with positive
pressure differences (flow in one direction) at the red end of
the spectrum and negative differences (flow in the opposite
direction) at the blue end. Thus, satur pressure differences (flow in one direction) at the red end of
the spectrum and negative differences (flow in the opposite
direction) at the blue end. Thus, saturated colours at either
end of the spectrum represent equal a the spectrum and negative differences (flow in the opposite
direction) at the blue end. Thus, saturated colours at either
end of the spectrum represent equal amplitudes, but opposite
directions. Green is in the middle at z direction) at the blue end. Thus, saturated colours at eithe
end of the spectrum represent equal amplitudes, but oppos
directions. Green is in the middle at zero and represents
pressure-difference amplitudes at or below me end of the spectrum represent equal amplitudes, but opposite
directions. Green is in the middle at zero and represents
pressure-difference amplitudes at or below measured estimates
of threshold sensitivity (0.002 Pa/2 mm directions. Green is in the middle at zero and represents
pressure-difference amplitudes at or below measured estimat
of threshold sensitivity $(0.002 \text{ Pa}/2 \text{ mm or } 0.001 \text{ m s}^{-2})$ for
individual posterior lateral line nerv pressure-difference amplitudes at or below measured estimates
of threshold sensitivity $(0.002 \text{ Pa}/2 \text{ mm or } 0.001 \text{ m s}^{-2})$ for
individual posterior lateral line nerve fibres. Axes *x*, *y* and *z*
are scaled in units of m of threshold sensitivity (0.002 Pa/2 mm or 0.001 ms⁻²) for individual posterior lateral line nerve fibres. Axes x, y and z

are scaled in units of metres.
movement until they are close enough to launch their ¢nal strike (Hoekstra & Janssen 1985). In visually movement until they are close enough to launch their
final strike (Hoekstra & Janssen 1985). In visually
deprived animals, the initial orientating and approach
hebaviour requires the lateral line (Hoekstra & Janssen final strike (Hoekstra & Janssen 1985). In visually
deprived animals, the initial orientating and approach
behaviour requires the lateral line (Hoekstra & Janssen
1985: Coombs & Conley 1997*a*: Braun & Coombs this deprived animals, the initial orientating and approach
behaviour requires the lateral line (Hoekstra & Janssen
1985; Coombs & Conley 1997*a*; Braun & Coombs, this
issue) and relies beavily if not exclusively on canal behaviour requires the lateral line (Hoekstra & Janssen
1985; Coombs & Conley 1997a; Braun & Coombs, this
issue) and relies heavily, if not exclusively, on canal,
rather than superficial neuromasts (S. Coombs, C. B. 1985; Coombs & Conley 1997a; Braun & Coombs, this issue) and relies heavily, if not exclusively, on canal, rather than superficial neuromasts (S. Coombs, C. B. Braun and B. Donovan unpublished data). Fortunately issue) and relies heavily, if not exclusively, on canal, rather than superficial neuromasts (S. Coombs, C. B.
Braun and B. Donovan, unpublished data). Fortunately
for us, the prev-capture behaviour can be elicited in the rather than superficial neuromasts (S. Coombs, C. B.
Braun and B. Donovan, unpublished data). Fortunately
for us, the prey-capture behaviour can be elicited in the

Figure 2. Illustration of how lateral line excitation patterns along the head and body of a mottled sculpin change Figure 2. Illustration of how lateral line excitation patterns
along the head and body of a mottled sculpin change
during an actual prey-capture event, from the time of signal
onset (a) to the time of strike (c). Each col along the head and body of a mottled sculpin change
during an actual prey-capture event, from the time of
onset (*a*) to the time of strike (*c*). Each coloured dot
represents the excitatory input (see figure for explanat during an actual prey-capture event, from the time of signal
onset (*a*) to the time of strike (*c*). Each coloured dot
represents the excitatory input (see figure for explanation of
colour code) to different neuromasts h onset (*a*) to the time of strike (c) . Each coloured dot
represents the excitatory input (see figure for explanation of
colour code) to different neuromasts housed in one of five canals on the head (supra- and infraorbital canals colour code) to different neuromasts housed in one of
five canals on the head (supra- and infraorbital canals
above and below the eye, the preopercular canal along the
cheek, the mandibular canal along the lower jaw, the five canals on the head (supra- and infraorbital canals
above and below the eye, the preopercular canal along t
cheek, the mandibular canal along the lower jaw, the
temporal canal across the top of the head) or in the true above and below the eye, the preopercular canal along the
cheek, the mandibular canal along the lower jaw, the
temporal canal across the top of the head) or in the trunk
canal along the body. Neuromasts in all canals are m cheek, the mandibular canal along the lower jaw, the
temporal canal across the top of the head) or in the trunk
canal along the body. Neuromasts in all canals are most easily seen in (a) , which affords a frontal view of the fish. canal along the body. Neuromasts in all canals are most
easily seen in (a) , which affords a frontal view of the fish.
The position of the fish relative to the source was mapped
in Cartesian coordinates from a digitized v easily seen in (a) , which affords a frontal view of the fish.
The position of the fish relative to the source was mapped
in Cartesian coordinates from a digitized video image of the
fish at each step in the pathway and l The position of the fish relative to the source was mapped
in Cartesian coordinates from a digitized video image of the
fish at each step in the pathway and, likewise, the Cartesian
coordinates of each canal pore relative in Cartesian coordinates from a digitized video image of the fish at each step in the pathway and, likewise, the Cartesian coordinates of each canal pore relative to the tip of the fish's sport were determined by using an fish at each step in the pathway and, likewise, the Cartesian coordinates of each canal pore relative to the tip of the fish's snout were determined by using an ocular micrometer on a stereomicroscope. stereomicroscope.

Laboratory from blinded animals with a chemically inert,
artificial prev source—a bite-size (6 mm in diameter) laboratory from blinded animals with a chemically inert,
artificial prey source—a bite-size (6 mm in diameter),
vibrating sphere This has made it possible for us to drive laboratory from blinded animals with a chemically inert,
artificial prey source—a bite-size (6 mm in diameter),
vibrating sphere. This has made it possible for us to drive
the behaviour with mechanosensory cues alone to us artificial prey source—a bite-size $(6 \text{ mm in diameter})$, vibrating sphere. This has made it possible for us to drive the behaviour with mechanosensory cues alone, to use the vibrating sphere. This has made it possible for us to drive
the behaviour with mechanosensory cues alone, to use the
same stimulus source in physiological and behavioural
experiments and to use a set of dipole field equati the behaviour with mechanosensory cues alone, to use the same stimulus source in physiological and behavioural experiments, and to use a set of dipole field equations for characterizing the stimulus field and for modelling same stimulus source in physiological and behavioural
experiments, and to use a set of dipole field equations for
characterizing the stimulus field and for modelling excita-
tion patterns along lateral line canal neuromast experiments, and to use a set of dipole field equations for
characterizing the stimulus field and for modelling excita-
tion patterns along lateral line canal neuromasts.

2. ASSUMPTIONS AND VALIDITY OF THE
MODELLING ARRROACH MPTIONS AND VALIDITY OF
MODELLING APPROACH

E. ASSUMPTIONS AND VALIDITY OF THE

MODELLING APPROACH

Static models of lateral line excitation patterns are

mputed at the time of maximum sphere excursion and Static models of lateral line excitation patterns are
computed at the time of maximum sphere excursion and
are based on several simplifying assumptions including Static models of lateral line excitation patterns are
computed at the time of maximum sphere excursion and
are based on several simplifying assumptions, including
(i) that the stimulus field is ideal and unbounded (i.e. computed at the time of maximum sphere excursion and
are based on several simplifying assumptions, including
(i) that the stimulus field is ideal and unbounded (i.e.
tank walls and fish's hody have no effect on the stimulu are based on several simplifying assumptions, including

(i) that the stimulus field is ideal and unbounded (i.e.

tank walls and fish's body have no effect on the stimulus

field): (ii) the quantities kg and kg are both (i) that the stimulus field is ideal and unbounded (i.e. tank walls and fish's body have no effect on the stimulus field); (ii) the quantities *ka* and *kr* are both much less than 1 where *k* is the acoustic wave number field); (ii) the quantities *ka* and *kr* are both much less than 1, where *k* is the acoustic wave number $(k = w/c)$, where *c* is sound speed and *w* is circular frequency), *a* is the source radius, and *r* is the distanc than 1, where *k* is the acoustic wave number $(k = w/c)$,
where *c* is sound speed and *w* is circular frequency), *a* is
the source radius, and *r* is the distance from the source;
(iii) there is a single sensory organ (neu where ϵ is sound speed and w is circular frequency), α is the source radius, and r is the distance from the source;
(iii) there is a single sensory organ (neuromast) between
every two pores on any given lateral the source radius, and r is the distance from the source;
(iii) there is a single sensory organ (neuromast) between
every two pores on any given lateral line canal; and
(iv) the response of each neuromast to fluid motio (iii) there is a single sensory organ (neuromast) between
every two pores on any given lateral line canal; and
(iv) the response of each neuromast to fluid motions
inside the canal is proportional to the outside pressure every two pores on any given lateral line canal; and
(iv) the response of each neuromast to fluid motions
inside the canal is proportional to the outside pressure
difference between the two pores, which is also propor-(iv) the response of each neuromast to fluid motions
inside the canal is proportional to the outside pressure
difference between the two pores, which is also proporinside the canal is proportional to the outside pressure
difference between the two pores, which is also propor-
tional to the acceleration of the surrounding water
(Denton & Grav 1983) difference between the t
tional to the accelerati
(Denton & Gray 1983).
The newest version of mal to the acceleration of the surrounding water
Venton & Gray 1983).
The newest version of the model computes the final
mulus to each canal neuromast as the difference

(Denton & Gray 1983).
The newest version of the model computes the final
stimulus to each canal neuromast as the difference between the acceleration of the fish's body and the local stimulus to each canal neuromast as the difference
between the acceleration of the fish's body and the local
accelerations of the surrounding water at the location of
the neuromast Euler's equation and the average pressure between the acceleration of the fish's body and the local
accelerations of the surrounding water at the location of
the neuromast. Euler's equation and the average pressure
along the top/bottom_rostral/caudal_and_left/righ accelerations of the surrounding water at the location of
the neuromast. Euler's equation and the average pressure
along the top/bottom, rostral/caudal and left/right sides
of the fish's body are used to determine the whol the neuromast. Euler's equation and the average pressure
along the top/bottom, rostral/caudal and left/right sides
of the fish's body are used to determine the whole-body along the top/bottom, rostral/caudal and left/right sides
of the fish's body are used to determine the whole-body
accelerations of the fish, which is treated as a rigid
cylinder of approximately the same dimensions of the fish's body are used to determine the whole-body
accelerations of the fish, which is treated as a rigid
cylinder of approximately the same dimensions
 $(20 \text{ mm} \times 15100 \text{ mm})$ and density (1072 km^{-3}) as the accelerations of the fish, which is treated as a rigid
cylinder of approximately the same dimensions
(20 mm × 15 100 mm) and density (1072 kg m⁻³) as the
mottled sculpin Local accelerations of the surrounding cylinder of approximately the same dimensions (20 mm × 15 100 mm) and density (1072 kg m⁻³) as the mottled sculpin. Local accelerations of the surrounding water are likewise determined from Fuler's equation and (20 mm \times 15 100 mm) and density (1072 kg m⁻³) as the mottled sculpin. Local accelerations of the surrounding water are likewise determined from Euler's equation and the pressure difference between canal pores mottled sculpin. Local accelerations of the surrounding water are likewise determined from Euler's equation and the pressure difference between canal pores. ter are likewise determined from Euler's equation and
e pressure difference between canal pores.
To test the validity of some these assumptions, we used
vsiological techniques to compare response patterns of

the pressure difference between canal pores.
To test the validity of some these assumptions, we used
physiological techniques to compare response patterns of
single peripheral lateral line nerve fibres to our modelled To test the validity of some these assumptions, we used
physiological techniques to compare response patterns of
single peripheral lateral line nerve fibres to our modelled
predictions. In essence, we used the fish and ind physiological techniques to compare response patterns of single peripheral lateral line nerve fibres to our modelled predictions. In essence, we used the fish and individual single peripheral lateral line nerve fibres to our modelled
predictions. In essence, we used the fish and individual
posterior lateral line nerve fibres innervating the trunk
canal as our stimulus measurement device so tha predictions. In essence, we used the fish and individual
posterior lateral line nerve fibres innervating the trunk
canal as our stimulus measurement device, so that both
the fish's presence and the presence of experimental posterior lateral line nerve fibres innervating the trunk
canal as our stimulus measurement device, so that both
the fish's presence and the presence of experimental tank
walls were automatically taken into account. Rather canal as our stimulus measurement device, so that both
the fish's presence and the presence of experimental tank
walls were automatically taken into account. Rather the fish's presence and the presence of experimental tank
walls were automatically taken into account. Rather
than taking the technically difficult approach of simulta-
neously recording responses from an array of fibres walls were automatically taken into account. Rather
than taking the technically difficult approach of simulta-
neously recording responses from an array of fibres
innervating canal neuromasts at different locations along than taking the technically difficult approach of simulta-
neously recording responses from an array of fibres
innervating canal neuromasts at different locations along
the canal to a fixed source location, we reversed the neously recording responses from an array of fibres
innervating canal neuromasts at different locations along
the canal to a fixed source location, we reversed the
frame of reference. That is we recorded the response of innervating canal neuromasts at different locations along
the canal to a fixed source location, we reversed the
frame of reference. That is, we recorded the response of
a single fibre innervating a single neuromast at a fi the canal to a fixed source location, we reversed the frame of reference. That is, we recorded the response of a single fibre innervating a single neuromast at a fixed location to a dinole source that slowly changed its lo frame of reference. That is, we recorded the response of a single fibre innervating a single neuromast at a fixed location to a dipole source that slowly changed its locaa single fibre innervating a single neuromast at a fixed
location to a dipole source that slowly changed its loca-
tion along the length of the canal. The results from this
experimental approach revealed that neural respon location to a dipole source that slowly changed its location along the length of the canal. The results from this experimental approach revealed that neural responses from many different fibres in both goldfish and sculpin from along the length of the canal. The results from this
experimental approach revealed that neural responses
from many different fibres in both goldfish and sculpin
followed both pressure difference applitude and direcexperimental approach revealed that neural responses
from many different fibres in both goldfish and sculpin
followed both pressure-difference amplitude and direcfrom many different fibres in both goldfish and sculpin
followed both pressure-difference amplitude and direc-
tion (phase) predictions of the model rather faithfully,
despite the presence of the fish and surrounding tank followed both pressure-difference amplitude and direction (phase) predictions of the model rather faithfully, despite the presence of the fish and surrounding tank walls (Coombs ℓt al. 1996; Coombs ℓt Conley 1997b) tion (phase) predictions of the model rather faithfully, despite the presence of the fish and surrounding tank walls (Coombs *et al.* 1996; Coombs & Conley 1997*b*). *Phil. Trans. R. Soc. Lond.* B (2000)

These physiological demonstrations give us confidence
that our model while still crude and assumption limited These physiological demonstrations give us confidence
that our model, while still crude and assumption limited,
is a reasonable first approximation of peripheral lateral These physiological demonstrations give us confidence
that our model, while still crude and assumption limited,
is a reasonable first approximation of peripheral lateral
line excitation patterns under controlled experiment that our model, while still crude and assumption limited, is a reasonable first approximation of peripheral lateral line excitation patterns under controlled experimental conditions.

3. INFORMATION ENCODING BY LATERAL LINE
EXCITATION BATTERNS TION ENCODING BY LATER.
EXCITATION PATTERNS

S. INFORMATION ENCODING BT EXTERNE LINE
EXCITATION PATTERNS
Newly modelled excitation patterns for a linear array of
nal neuromasts at different distances from the source EXCHATION FATTENNS

SENSITY CONTRACTED SERVERT AND RELATION TO THE SOURCE CAN CONTRACTED AT A SUITE AND SUITE AND THE SOURCE THE SOURC canal neuromasts at different distances from the source are quite similar to older models (e.g. Coombs *et al.* 1996) canal neuromasts at different distances from the source
are quite similar to older models (e.g. Coombs *et al.* 1996)
in showing that information about source azimuth is
contained in the location of the maximum pressureare quite similar to older models (e.g. Coombs *et al.* 1996) in showing that information about source azimuth is contained in the location of the maximum pressure-
difference amplitude whereas information about source contained in the location of the maximum pressure-
difference amplitude, whereas information about source contained in the location of the maximum pressure-
difference amplitude, whereas information about source
distance is contained in the spread of excitation
(figure $|a\rangle$) Thus unlike visual images which get smaller difference amplitude, whereas information about source
distance is contained in the spread of excitation
(figure 1*a*). Thus, unlike visual images, which get smaller
as the source gets further away hydrodynamic images get distance is contained in the spread of excitation (figure la). Thus, unlike visual images, which get smaller as the source gets further away, hydrodynamic images get larger as do electrosensory images (yon der Emde *et a* (figure 1*a*). Thus, unlike visual images, which get smaller as the source gets further away, hydrodynamic images get larger, as do electrosensory images (von der Emde *et al.* 1998). This relatively unusual distance cue i larger, as do electrosensory images (von der Emde *et al.* 1998). This relatively unusual distance cue is theoretically robust and unambiguous; that is, if source amplitude or size is increased at a given distance, the lev 1998). This relatively unusual distance cue is theoretically robust and unambiguous; that is, if source amplitude or size is increased at a given distance, the level but not the robust and unambiguous; that is, if source amplitude or
size is increased at a given distance, the level but not the
spread of excitation increases (e.g. compare the excitation
pattern for a small source 4cm away in figure size is increased at a given distance, the level but not the spread of excitation increases (e.g. compare the excitation pattern for a small source 4 cm away in figure 1*a* with that of a large source at the same dist spread of excitation increases (e.g. compare the excitation pattern for a small source 4 cm away in figure 1*b* with that of a large source at the same distance in figure 1*b*). Thus even though neak excitation levels may pattern for a small source 4 cm away in figure $1a$ with that of a large source at the same distance in figure $1b$). Thus, even though peak excitation levels may be the same that of a large source at the same distance in figure $1b$).
Thus, even though peak excitation levels may be the same
for a distant, high-amplitude (or large) source and a
nearby low-amplitude (or small) source there is s Thus, even though peak excitation levels may be the same
for a distant, high-amplitude (or large) source and a
nearby, low-amplitude (or small) source, there is sufficient
information in the spread of excitation to disting for a distant, high-amplitude (or large) source and a
nearby, low-amplitude (or small) source, there is sufficient
information in the spread of excitation to distinguish
between the two (e.g. compare the excitation patter nearby, low-amplitude (or small) source, there is sufficient
information in the spread of excitation to distinguish
between the two (e.g. compare the excitation pattern for information in the spread of excitation to distinguish
between the two (e.g. compare the excitation pattern for
a large source 4 cm away in figure 1*b* with that for a
smaller source 1 cm away in figure 1*a*) between the two (e.g. compare the exc
a large source 4 cm away in figure 1
smaller source 1 cm away in figure 1*a*). **4. UNDERSTANDING AND PREDICTING BEHAVIOUR**

By setting model parameters (e.g. fish length, interpore distances, threshold levels of excitation for peripheral By setting model parameters (e.g. fish length, interpore
distances, threshold levels of excitation for peripheral
lateral line nerve fibres, etc.—see figure 1 legend) to
empirically determined values for the mottled sculpi distances, threshold levels of excitation for peripheral
lateral line nerve fibres, etc.—see figure 1 legend) to
empirically determined values for the mottled sculpin, it
also becomes possible to understand behavioural per lateral line nerve fibres, etc.—see figure 1 legend) to empirically determined values for the mottled sculpin, it also becomes possible to understand behavioural perfor-
mance in terms of excitation patterns. For example, empirically determined values for the mottled sculpin, it also becomes possible to understand behavioural performance in terms of excitation patterns. For example, the maximum distance at which the unconditioned orienmance in terms of excitation patterns. For example, the maximum distance at which the unconditioned orientating response of the mottled sculpin can be reliably evoked from a given dipole source (that modelled in maximum distance at which the unconditioned orientating response of the mottled sculpin can be reliably evoked from a given dipole source (that modelled in figure 1*a*) has been measured to be *ca*, $11-12$ cm (Coombs) tating response of the mottled sculpin can be reliably
evoked from a given dipole source (that modelled in
figure $|a\rangle$ has been measured to be *ca*. $11-12$ cm (Coombs
1999: Braun & Coombs, this issue). At these distanc evoked from a given dipole source (that modelled in figure 1*a*) has been measured to be *ca*. $11-12$ cm (Coombs 1999; Braun & Coombs, this issue). At these distances, excitation levels range from physiologically measure figure 1a) has been measured to be *ca*. $11-12$ cm (Coombs 1999; Braun & Coombs, this issue). At these distances, excitation levels range from physiologically measured threshold levels (0.002 $Pa/2$ mm) at the head and ta 1999; Braun & Coombs, this issue). At these distances, excitation levels range from physiologically measured threshold levels $(0.002 \text{ Pa}/2 \text{ mm})$ at the head and tail to approximately twice the physiological threshold at excitation levels range from physiologically measured
threshold levels $(0.002 \text{ Pa}/2 \text{ mm})$ at the head and tail to
approximately twice the physiological threshold at mid-
body locations. Relative to excitation patterns mo approximately twice the physiological threshold at midapproximately twice the physiological threshold at mid-
body locations. Relative to excitation patterns modelled
for closer source locations, where peak excitation levels are
several orders of magnitude above the threshold body locations. Relative to excitation patterns modelled
for closer source locations, where peak excitation levels are
several orders of magnitude above the threshold, the
excitation pattern at this threshold distance is r for closer source locations, where peak excitation levels are
several orders of magnitude above the threshold, the
excitation pattern at this threshold distance is relatively
flat (figure $|a\rangle$) Changes in excitation pat several orders of magnitude above the threshold, the excitation pattern at this threshold distance is relatively flat (figure 1*a*). Changes in excitation patterns as a function of source distance also predict that informa excitation pattern at this threshold distance is relatively
flat (figure la). Changes in excitation patterns as a function
of source distance also predict that information about
source location, and therefore the ability o flat (figure la). Changes in excitation patterns as a function of source distance also predict that information about source location, and therefore the ability of sculpin to of source distance also predict that information about
source location, and therefore the ability of sculpin to
pinpoint the exact location of the source, will get increas-
ingly better at shorter distances. Not only do re source location, and therefore the ability of sculpin to
pinpoint the exact location of the source, will get increas-
ingly better at shorter distances. Not only do regions of
maximum excitation become narrower and more st pinpoint the exact location of the source, will get increasingly better at shorter distances. Not only do regions of maximum excitation become narrower and more steeply sloped but also the delineation of these regions at ingly better at shorter distances. Not only do regions of maximum excitation become narrower and more steeply sloped, but also the delineation of these regions at maximum excitation become narrower and more steeply
sloped, but also the delineation of these regions at
distances less than *ca*. 6 cm is even further enhanced by
surrounding regions of excitation in the opposite directio sloped, but also the delineation of these regions at distances less than ca . 6 cm is even further enhanced by surrounding regions of excitation in the opposite direction.
The fact that over 90% of all successful strikes distances less than ca . 6 cm is even further enhanced by
surrounding regions of excitation in the opposite direction.
The fact that over 90% of all successful strikes are made

BIOLOGICAL
SCIENCES

THE ROYAL B

**PHILOSOPHICAL
TRANSACTIONS
TRANSACTIONS**

1114 S. Coombs and others Lateral line imaging
from distances less than 4 cm, with the mean strike from distances less than 4 cm, with the mean strike
distance just under 2 cm (Coombs & Conley 1997*a*),
certainly supports the idea that information about source from distances less than 4 cm, with the mean strike
distance just under 2 cm (Coombs & Conley 1997*a*),
certainly supports the idea that information about source
location is hest at these close distances certainly supports the idea that information about source
location is best at these close distances.

To determine if other aspects of prey-capture behaviour location is best at these close distances.
To determine if other aspects of prey-capture behaviour
could be explained on the basis of peripheral excitation
natterns we videotaned the annroach behaviour of mottled To determine if other aspects of prey-capture behaviour
could be explained on the basis of peripheral excitation
patterns, we videotaped the approach behaviour of mottled
sculpin for different starting distances and orient could be explained on the basis of peripheral excitation all of which converge at approximately the same location
patterns, we videotaped the approach behaviour of mottled on the side of the fish's head. In this regard, it patterns, we videotaped the approach behaviour of mottled
sculpin for different starting distances and orientations in
over 400 trials (Coombs & Conley 1997*a*). Approach path-
wavs depended largely on the initial starting sculpin for different starting distances and orientations in
over 400 trials (Coombs & Conley 1997a). Approach path-
ways depended largely on the initial starting position. Fish
pointing towards the source at the time of s over 400 trials (Coombs & Conley 1997a). Approach pathways depended largely on the initial starting position. Fish
pointing towards the source at the time of signal onset
tended to approach the source indirectly—either in ways depended largely on the initial starting position. Fish
pointing towards the source at the time of signal onset
tended to approach the source indirectly—either in an
arching pattern in which the fish kent the source t pointing towards the source at the time of signal onset
tended to approach the source indirectly—either in an
arching pattern in which the fish kept the source to one side
of its body or in a zigzag fashion in which the fi tended to approach the source indirectly—either in an arching pattern in which the fish kept the source to one side
of its body or in a zigzag fashion in which the fish alter-
nated between keeping the source to the left a arching pattern in which the fish kept the source to one side
of its body or in a zigzag fashion in which the fish alter-
nated between keeping the source to the left and right sides
of its body When the source was at the of its body or in a zigzag fashion in which the fish alternated between keeping the source to the left and right sides
of its body. When the source was at the fish's side at signal
onset, however, approach pathways tended, nated between keeping the source to the left and right sides
of its body. When the source was at the fish's side at signal
onset, however, approach pathways tended to be more
direct and involved fewer stens (figure 2). In of its body. When the source was at the fish's side at signal
onset, however, approach pathways tended to be more
direct and involved fewer steps (figure 2). In a few of these
cases, the initial orientating response was al onset, however, approach pathways tended to be more
direct and involved fewer steps (figure 2). In a few of these
cases, the initial orientating response was also the final
strike response and of these successful long-dist direct and involved fewer steps (figure 2). In a few of these
cases, the initial orientating response was also the final
strike response, and of these successful long-distance
strikes (greater than one standard deviation a cases, the initial orientating response was also the final
strike response, and of these successful long-distance
strikes (greater than one standard deviation above the
mean strike distance) 75% were elicited by laterally strike response, and of these successful long-distance
strikes (greater than one standard deviation above the
mean strike distance), 75% were elicited by laterally strikes (greater than one standard deviation above the
mean strike distance), 75% were elicited by laterally
located sources (e.g. figure 2*b*). In contrast, 83% of
unsuccessful strikes (within the mean strike distance) we mean strike distance), 75% were elicited by laterally located sources (e.g. figure $2b$). In contrast, 83% of unsuccessful strikes (within the mean strike distance) were associated with frontally located sources located sources (e.g. figure 2*b*). In counsuccessful strikes (within the mean strik
associated with frontally located sources. associated with frontally located sources.
5. UNILATERAL PROCESSING

The general orientating and approach strategies of the mottled sculpin—one step and one side at a time—are The general orientating and approach strategies of the
mottled sculpin—one step and one side at a time—are
consistent with the idea that sculpin are able to extract
information about both source distance and azimuth mottled sculpin—one step and one side at a time—are
consistent with the idea that sculpin are able to extract
information about both source distance and azimuth
from excitation patterns along a single unilateral sensory consistent with the idea that sculpin are able to extract
information about both source distance and azimuth
from excitation patterns along a single unilateral sensory
surface. This idea is further supported by experiments information about both source distance and azimuth
from excitation patterns along a single unilateral sensory
surface. This idea is further supported by experiments in
which unilateral deneryations of specific regions (e. from excitation patterns along a single unilateral sensory
surface. This idea is further supported by experiments in
which unilateral denervations of specific regions (e.g.
head versus trunk) of the lateral line caused sit surface. This idea is further supported by experiments in which unilateral denervations of specific regions (e.g. head versus trunk) of the lateral line caused site-specific deficits corresponding to the region of denervat which unilateral denervations of specific regions (e.g. head versus trunk) of the lateral line caused site-specific deficits corresponding to the region of denervation, but head versus trunk) of the lateral line caused site-specific
deficits corresponding to the region of denervation, but
did not otherwise interfere with the sculpin's ability to
localize sources on the intact side or near the deficits corresponding to the region of denervation, but
did not otherwise interfere with the sculpin's ability to
localize sources on the intact side or near the intact
regions of the denervated side (Conley & Coombs 1998 did not otherwise interfere with the sculpin's ability to localize sources on the intact side or near the intact
regions of the denervated side (Conley & Coombs 1998).
Examples of poor performance (misses) for frontal localize sources on the intact side or near the intact
regions of the denervated side (Conley & Coombs 1998).
Examples of poor performance (misses) for frontal regions of the denervated side (Conley & Coombs 1998).
Examples of poor performance (misses) for frontal
sources also suggest that sensory representations on the
left and right side of the animal may not be integrated Examples of poor performance (misses) for frontal
sources also suggest that sensory representations on the
left and right side of the animal may not be integrated
centrally to form frontal images of sensory space sources also suggest that sensory representations on the
left and right side of the animal may not be integrated
centrally to form frontal images of sensory space,
although it is also possible that peripheral morphology left and right side of the animal may not be integrated
centrally to form frontal images of sensory space,
although it is also possible that peripheral morphology centrally to form frontal images of sensory space,
although it is also possible that peripheral morphology
(e.g. frontal blind spot) may contribute to this poor
performance. So, unlike the vertebrate visual system although it is also possible that peripheral morphology
(e.g. frontal blind spot) may contribute to this poor
performance. So, unlike the vertebrate visual system,
which uses both eves to provide depth of field or the (e.g. frontal blind spot) may contribute to this poor
performance. So, unlike the vertebrate visual system,
which uses both eyes to provide depth of field, or the
auditory system of terrestrial vertebrates which computes performance. So, unlike the vertebrate visual system,
which uses both eyes to provide depth of field, or the source azimuth from time and/or intensity differences at the two ears, the lateral line system theoretically deterauditory system of terrestrial vertebrates, which computes source azimuth from time and/or intensity differences at
the two ears, the lateral line system theoretically deter-
mines both azimuth and distance from a single unilateral
sensory surface the two ears, the
mines both azimu
sensory surface.
Indirect appr Indirect approach and distance from a single unilateral
Indirect approach pathways, poor performance
isses) for frontal sources and exceptional performance

sensory surface.

Indirect approach pathways, poor performance

(misses) for frontal sources, and exceptional performance ('far' strikes and direct paths) for lateral sources, all indicate that it is advantageous for fish to expose their ('far' strikes and direct paths) for lateral sources, all indicate that it is advantageous for fish to expose their lateral sensory surfaces to the source. On theoretical grounds a lateral exposure would confer at least t indicate that it is advantageous for fish to expose their
lateral sensory surfaces to the source. On theoretical
grounds, a lateral exposure would confer at least two
advantages maximizing (i) the amount and breadth of lateral sensory surfaces to the source. On theoretical
grounds, a lateral exposure would confer at least two
advantages, maximizing (i) the amount and breadth of
stimulus field information that could be represented on a grounds, a lateral exposure would confer at least two
advantages, maximizing (i) the amount and breadth of
stimulus field information that could be represented on a
given side of the fish by virtue of the fact that the advantages, maximizing (i) the amount and breadth of
stimulus field information that could be represented on a
given side of the fish by virtue of the fact that the
maiority of lateral line organs, as the name suggests, ar stimulus field information that could be represented on a
given side of the fish by virtue of the fact that the
majority of lateral line organs, as the name suggests, are majority of lateral line organs, as the name suggests, are
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located on the sides of the animal's body, and (ii) the potential use of a three-dimensional sampling system that located on the sides of the animal's body, and (ii) the potential use of a three-dimensional sampling system that includes the rostrocaudally orientated trunk and supralocated on the sides of the animal's body, and (ii) the potential use of a three-dimensional sampling system that includes the rostrocaudally orientated trunk and supra-
orbital canals the dorsoventrally orientated preoper potential use of a three-dimensional sampling system that
includes the rostrocaudally orientated trunk and supra-
orbital canals, the dorsoventrally orientated preopercular includes the rostrocaudally orientated trunk and supra-
orbital canals, the dorsoventrally orientated preopercular
canal and the lateromedially orientated temporal canal—
all of which converge at approximately the same loc orbital canals, the dorsoventrally orientated preopercular
canal and the lateromedially orientated temporal canal—
all of which converge at approximately the same location
on the side of the fish's head. In this regard, it canal and the lateromedially orientated temporal canal—
all of which converge at approximately the same location
on the side of the fish's head. In this regard, it is inter-
esting to note that weakly electric black ghost all of which converge at approximately the same location
on the side of the fish's head. In this regard, it is inter-
esting to note that weakly electric black ghost knifefish
tend to approach their prev with the dorsal su on the side of the fish's head. In this regard, it is interesting to note that weakly electric black ghost knifefish
tend to approach their prey with the dorsal surface of the
fish forming the leading edge as the fish move esting to note that weakly electric black ghost knifefish
tend to approach their prey with the dorsal surface of the
fish forming the leading edge as the fish moves through
the water (Nelson & Maciver 1999) Leading with th tend to approach their prey with the dorsal surface of the
fish forming the leading edge as the fish moves through
the water (Nelson & Maciver 1999). Leading with the
dorsal edge is thought to have several advantages fish forming the leading edge as the fish moves through
the water (Nelson & Maciver 1999). Leading with the
dorsal edge is thought to have several advantages,
including optimizing the exposure of dorsally situated the water (Nelson & Maciver 1999). Leading with the
dorsal edge is thought to have several advantages,
including optimizing the exposure of dorsally situated
electrosensory recentors, which are two to three times dorsal edge is thought to have several advantages,
including optimizing the exposure of dorsally situated
electrosensory receptors, which are two to three times
more dense on the dorsal surface than on ventral or electrosensory receptors, which are two to three times
more dense on the dorsal surface than on ventral or electrosensory receptors, which are two to three times
more dense on the dorsal surface than on ventral or
lateral surfaces. Thus, active positioning of receptor
surfaces whether they are dorsal in the case of the more dense on the dorsal surface than on ventral or
lateral surfaces. Thus, active positioning of receptor
surfaces, whether they are dorsal in the case of the
electrosensory system of the black ghost knifefish or lateral surfaces. Thus, active positioning of receptor
surfaces, whether they are dorsal in the case of the
electrosensory system of the black ghost knifefish, or
lateral in the case of the lateral line system of the mottl surfaces, whether they are dorsal in the case of the electrosensory system of the black ghost knifefish, or lateral in the case of the lateral line system of the mottled sculpin may help animals optimize the information electrosensory system of the black ghost knifefish, or lateral in the case of the lateral line system of the mottled sculpin, may help animals optimize the information content of incoming signals lateral in the case of the later:
sculpin, may help animals
content of incoming signals. content of incoming signals.
We thank research assistants Jim Collier, Debbie Eddison,

We thank research assistants Jim Collier, Debbie Eddison,
Marty Pryzdia and Brian Donovan for their help in collecting
and analysing the behavioural data and in taking care of the We thank research assistants Jim Collier, Debbie Eddison,
Marty Pryzdia and Brian Donovan for their help in collecting
and analysing the behavioural data and in taking care of the
fish Rocio limenez for her help in determi Marty Pryzdia and Brian Donovan for their help in collecting
and analysing the behavioural data and in taking care of the
fish, Rocio Jimenez for her help in determining the three-
dimensional coordinates of lateral line c and analysing the behavioural data and in taking care of the fish, Rocio Jimenez for her help in determining the three-dimensional coordinates of lateral line canal pores on the head fish, Rocio Jimenez for her help in determining the three-
dimensional coordinates of lateral line canal pores on the head
and body of mottled sculpin, and Dr Chris Braun for his
helpful comments on an earlier version of t dimensional coordinates of lateral line canal pores on the head
and body of mottled sculpin, and Dr Chris Braun for his
helpful comments on an earlier version of this manuscript. This
work was funded by a Program Project G and body of mottled sculpin, and Dr Chris Braun for his
helpful comments on an earlier version of this manuscript. This
work was funded by a Program Project Grant from the
National Institute on Deafness and Other Communica helpful comments on an earlier version of this manuscript. This
work was funded by a Program Project Grant from the
National Institute on Deafness and Other Communication
Disorders and by a grant from the Office of Naval R work was funded by a Program Project Grant from the National Institute on Deafness and Other Communicatio
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the mottled sculpin, *Co*
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