

cells contrasting interactions between mitral cells and ruffed Odour discrimination in the olfactory bulb of goldfish:

H. P. Zippel, M. Gloger, S. Nasser and S. Wilcke

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 Odour discrimination in the olfactory bulb of goldfish: contrasting interactions between **mitral cells and ruffed cells**

H. P. Zippel* **, M. Gloger, S. Nasser and S. Wilcke**

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Anatomical differences characterizing mitral cells and ruffed cells have been published by T. Kosaka and Anatomical differences characterizing mitral cells and ruffed cells have been published by T. Kosaka and
K. Hama in three teleost species. Physiological responses from both types of relay neurons were recorded
extracellula Anatomical differences characterizing mitral cells and ruffed cells have been published by T. Kosaka and K. Hama in three teleost species. Physiological responses from both types of relay neurons were recorded extracellula K. Hama in three teleost species. Physiological responses from both types of relay neurons were recorded extracellularly and simultaneously in the plexiform layer, using a single tungsten microelectrode. During interstimul extracellularly and simultaneously in the plexiform layer, using a single tungsten microelectrode. During
interstimulus intervals mitral cells responded with higher, frequently burst-like impulse rates triggered by
the act interstimulus intervals mitral cells responded with higher, frequently burst-like impulse rates triggered by
the activity of epithelial receptor neurons. Mitral cell activity could be totally suppressed by local
anaesthesi the activity of epithelial receptor neurons. Mitral cell activity could be totally suppressed by local anaesthesia of the olfactory epithelium. Ruffed cell impulse rates were low, and each action potential triggered a long anaesthesia of the olfactory epithelium. Ruffed cell impulse rates were low, and each action potential
triggered a long-lasting (3–5 ms), continuously varying, summed granule cell potential. During olfactory
stimulation wi triggered a long-lasting (3–5 ms), continuously varying, summed granule cell potential. During olfactory
stimulation with non-familiar stimuli and important biological stimuli such as amino acids, preovulatory
and ovulator stimulation with non-familiar stimuli and important biological stimuli such as amino acids, preovulatory
and ovulatory pheromones, and a probable alarm pheromone, contrasting interactions between mitral
cells and ruffed ce and ovulatory pheromones, and a probable alarm pheromone, contrasting interactions between mitral cells and ruffed cells were recorded frequently, which resulted in a drastic intensification of centrally transmitted inform cells and ruffed cells were recorded frequently, which resulted in a drastic intensification of centrally transmitted information. An excitation of mitral cells' activity via granule cells laterally inhibited the ruffed ce transmitted i:
ruffed cells' a
ruffed cells.

Keywords: goldfish; olfactory bulb; mitral cells; ruffed cells; electrophysiology

1. INTRODUCTION

1. INTRODUCTION
Goldfish as experimental animals offer a number of
physiological advantages: in higher vertebrates mitral **PHYSIOD CHON**
Goldfish as experimental animals offer a number of
physiological advantages: in higher vertebrates mitral
cells and tufted cells are located in different lavers: in Goldfish as experimental animals offer a number of
physiological advantages: in higher vertebrates mitral
cells and tufted cells are located in different layers; in
goldfish the two classes of bulbar relay neurons lie clos physiological advantages: in higher vertebrates mitral cells and tufted cells are located in different layers; in goldfish the two classes of bulbar relay neurons lie close cells and tufted cells are located in different layers; in
goldfish the two classes of bulbar relay neurons lie close
to each other in the plexiform layer. Simultaneous extra-
cellular recordings from both types of relay n goldfish the two classes of bulbar relay neurons lie close
to each other in the plexiform layer. Simultaneous extra-
cellular recordings from both types of relay neurons can
be made with a single tungsten electrode. Whethe to each other in the plexiform layer. Simultaneous extra-
cellular recordings from both types of relay neurons can
be made with a single tungsten electrode. Whether a
direct lateral inhibition via granule cells present in cellular recordings from both types of relay neurons can
be made with a single tungsten electrode. Whether a
direct lateral inhibition via granule cells present in gold-
fish also exists between different relay neurons in be made with a single tungsten electrode. Whether a
direct lateral inhibition via granule cells present in gold-
fish also exists between different relay neurons in
mammals (Nickell & Shinley 1992) is unknown direct lateral inhibition via granule cells present fish also exists between different relay neu
mammals (Nickell & Shipley 1992) is unknown.
In contrast to mitral cells (Kosaka & Hame fish also exists between different relay neurons in
mammals (Nickell & Shipley 1992) is unknown.
In contrast to mitral cells (Kosaka & Hama 1982),

mammals (Nickell & Shipley 1992) is unknown. in
In contrast to mitral cells (Kosaka & Hama 1982), ca
ruffed cells' glomerular dendrites have no input from tig
enithelial sensory neurons (Kosaka & Hama 1981–1982– In contrast to mitral cells (Kosaka & Hama 1982),
ruffed cells' glomerular dendrites have no input from
epithelial sensory neurons (Kosaka & Hama 1981, 1982–
1983) while sensors from the elfactory epithelium innerruffed cells' glomerular dendrites have no input from
epithelial sensory neurons (Kosaka & Hama 1981, 1982–
1983), while sensors from the olfactory epithelium inner-
vate both mitral and tufted cells. Anaesthesia of the ol epithelial sensory neurons (Kosaka & Hama 1981, 1982–1983), while sensors from the olfactory epithelium inner-
vate both mitral and tufted cells. Anaesthesia of the olfactory epithelium in goldfish therefore results in a blockade vate both mitral and tufted cells. Anaesthesia of the olfactory epithelium in goldfish therefore results in a blockade
of the driving input from spontaneously active receptor
neurons, and the activity of mitral cells is re tory epithelium in goldfish therefore results in a blockade
of the driving input from spontaneously active receptor
neurons, and the activity of mitral cells is reversibly
blocked. Consequently, a partial or total blockade blocked. Consequently, a partial or total blockade of neurons, and the activity of mitral cells is reversibly
blocked. Consequently, a partial or total blockade of
lateral inhibition from granule cells activated by mitral
cells results in a high and frequently rhythmic activi blocked. Consequently, a partial or total blockade of lateral inhibition from granule cells activated by mitral cells results in a high and frequently rhythmic activity of ruffed cells (Zinnel *et al* 1999) ruffed cells in a high and frequencells results in a high and frequence ruffed cells (Zippel *et al.* 1999). Ils results in a high and frequently rhythmic activity of
ffed cells (Zippel *et al.* 1999).
Each ruffed cell forms many initial pedunculate protru-
nps (IP 'ruff') from a long (70–950m) non-myelinated

ruffed cells (Zippel *et al.* 1999).
Each ruffed cell forms many initial pedunculate protrusions (IP 'ruff') from a long (70–250m) non-myelinated
portion of the axon (Kosaka & Hama 1979; Kosaka Each ruffed cell forms many initial pedunculate protrusions (IP 'ruff') from a long (70–250 m) non-myelinated
portion of the axon (Kosaka & Hama 1979; Kosaka
1980) 'The number of synapses on the IP is roughly sions (IP 'ruff') from a long $(70-250 \text{ m})$ non-myelinated
portion of the axon (Kosaka & Hama 1979; Kosaka
1980). 'The number of synapses on the IP is roughly estimated to be 1.000 to 2.000... asymmetrical' (excita-

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tory for granule cells)' synapses from the IP, 63%;
symmetrical' (inhibitory) 'synapses onto the IP 12% and tory for granule cells)' synapses from the IP, 63% ;
symmetrical' (inhibitory) 'synapses onto the IP, 12% , and
reciprocal synapses 25% ' (Kosaka 1980, p. 119). Theretory for granule cells)' synapses from the IP, 63% ;
symmetrical' (inhibitory) 'synapses onto the IP, 12% , and
reciprocal synapses, 25% ' (Kosaka 1980, p.119). There-
fore from mitral cells single action notentials symmetrical' (inhibitory) 'synapses onto the IP, 12%, and
reciprocal synapses, 25%' (Kosaka 1980, p.119). There-
fore, from mitral cells, single action potentials $(1-1.5 \text{ ms})$
or bursts were recorded whilst a $1.0-1.5 \text{$ reciprocal synapses, 25% (Kosaka 1980, p.119). Therefore, from mitral cells, single action potentials $(1-1.5 \text{ ms})$
or bursts were recorded, whilst a $1.0-1.5 \text{ ms}$ ruffed cell
action potential always triggered a summe fore, from mitral cells, single action potentials $(1-1.5 \text{ ms})$
or bursts were recorded, whilst a $1.0-1.5 \text{ ms}$ ruffed cell
action potential always triggered a summed granule cell or bursts were recorded, whilst a 1.0–1.5 ms ruffed cell
action potential always triggered a summed granule cell
potential of 3 ms duration. Steps in the summed granule
cell potential were never recorded i.e. the ruffed ce action potential always triggered a summed granule cell
potential of 3 ms duration. Steps in the summed granule
cell potential were never recorded, i.e. the ruffed cells'
action potential always triggered via the IP a smal potential of 3 ms duration. Steps in the summed granule
cell potential were never recorded, i.e. the ruffed cells'
action potential always triggered via the IP a smaller or
greater pool of granule cells. Triggering of the cell potential were never recorded, i.e. the ruffed cells'
action potential always triggered via the IP a smaller or
greater pool of granule cells. Triggering of the granule
cell potentials by the ruffed cells' action pote action potential always triggered via the IP a smaller or
greater pool of granule cells. Triggering of the granule
cell potentials by the ruffed cells' action potential resulted
in a constant 3 ms interval from neak to pea greater pool of granule cells. Triggering of the granule
cell potentials by the ruffed cells' action potential resulted
in a constant 3 ms interval from peak to peak. The signifi-
cantly different morphological features, e cell potentials by the ruffed cells' action potential resulted
in a constant 3 ms interval from peak to peak. The signifi-
cantly different morphological features, excellently invesin a constant 3 ms interval from peak to peak. The significantly different morphological features, excellently inves-
tigated by T. Kosaka and K. Hama, and their
physiological consequences (Zippel *et al* 1999) make it cantly different morphological features, excellently investigated by T. Kosaka and K. Hama, and their physiological consequences (Zippel *et al.* 1999), make it easy to discriminate mitral cell and ruffed cell notentials tigated by T. Kosaka and K. Hama, and their
physiological consequences (Zippel *et al.* 1999), make it
easy to discriminate mitral cell and ruffed cell potentials
during extracellular (not however during intracellular) physiological consequences (Zippel et al . 1999), make it easy to discriminate mitral cell and ruffed cell potentials during extracellular (not, however, during intracellular) recordings.

2. MATERIAL AND METHODS

2. MATERIAL AND METHODS
Potentials from the two different types of relay neurons could
recorded outpoolly and simultaneously in the playiform Be recorded extracellularly and simultaneously in the plexiform
layer wing a simela tungaten missingle destracel (AM gustame 5770) be recorded extracellularly and simultaneously in the plexiform
layer, using a single tungsten microelectrode (AM systems 5770; be recorded extracellularly and simultaneously in the plexiform
layer, using a single tungsten microelectrode (AM systems 5770;
S. W. Everett, WA, USA; 5-7M Ω). In contrast to higher verte-
hates in goldfish a great numb layer, using a single tungsten microelectrode (AM systems 5770;
S. W. Everett, WA, USA; 5–7 $\text{M}\Omega$). In contrast to higher verte-
brates, in goldfish a great number of non-familiar and important
natural stimuli, includi brates, in goldfish a great number of non-familiar and important natural stimuli, including pheromones, are structurally known (Zippel *et al.* 1993) and can be applied in defined molarities: natural stimuli, including pheromones, are structurally known
(Zippel *et al.* 1993) and can be applied in defined molarities:
(non-familiar stimuli: amyl acetate, β -ionone, 2-phenylethanol
 10^{-6} , relevant patural st 10^{-6} ; re bel *et al.* 1993) and can be applied in defined molarities:
familiar stimuli: amyl acetate, β -ionone, 2-phenylethanol;
relevant natural stimuli: four amino acids (L-Ala, L-Glu,
 μ , L, L, L, 10⁻⁶ to 10⁻¹⁰M; are a L-Arg, L-Lsy) 10^{-6} to 10^{-10} M; pre-ovulatory pheromones: in : amyl acetate, β -ionone, 2-phenylethanol
d stimuli: four amino acids (L-Ala, L-Glu,
to 10^{-10} M; pre-ovulatory pheromones: in

 $3(N)$ -oxide, the probable alarm pheromone in four different molarities and hypoxanthine. (*a*) 10^{-13} M: tonic excitation of M1 Figure 1. Simultaneous recordings from three mitral cells (M1–M3) and a ruffed cell (R) during application of hypoxanth
3(N)-oxide, the probable alarm pheromone in four different molarities and hypoxanthine. (*a*) 10^{-13} 3(N)-oxide, the probable alarm pheromone in four different molarities and hypoxanthine. (*a*) 10⁻¹³M: tonic excitation of N
and M2, R total inhibition. (*b*) 10⁻¹¹M: M1 phasic-tonic excitation, M2 strong excitation, M3 inhibition; (c) 10^{-9} M: M1 phasic-tonic excitation, M2 tonic excitation, M3 indifferent, R total inhibition. (d) 10^{-7} M: all mitral cells (M1–M3) are excited phasic, M2 and M3 are phasic tonic, and R is totally inhibi inhibition of M1 and M3, tonic excitation of M2, R total inhibition. Recordings present the last 60 s of the 180 s interstimulus phase and the 15 s during stimulus application; vertical bars represent the number of potential recorded per second.

electro-olfactogram (EOG) (Sorensen et al. 1990) highly effective electro-olfactogram (EOG) (Sorensen *et al.* 1990) highly effective
17, 20β-dihydroxyprogesterone $(10^{-9}$ to 10^{-11} M); 17, 20β-21-
trihydroxyprogesterone $(10^{-9}$ to 10^{-11} M) and in EOG electro-oltactogram (EOG) (Sorensen *et al.* 1990) highly effective

17, 20β-dihydroxyprogesterone $(10^{-9}$ to 10^{-11} M); 17, 20β-21-

trihydroxyprogesterone $(10^{-9}$ to 10^{-11} M), and in EOG a

(Sorensen *et al.* 1990) 17, 20β-dihydroxyprogesterone $(10^{-9}$ to 10^{-11} M); 17, 20β-21-
trihydroxyprogesterone $(10^{-9}$ to 10^{-11} M), and in EOG
(Sorensen *et al.* 1990) less effective 4-pregnen-20 α -ol 3-one $(10^{-7}$
to 10^{-9} M) 4 pregnen trihydroxyprogesterone (10^{-9} to 10^{-11} M), and in EOG
(Sorensen *et al.* 1990) less effective 4-pregnen-20 α -ol-3-one (10^{-7}
to 10^{-9} M), 4-pregnen-20 β -ol-3-one, dihydroxyprogesterol, and
andreated ione (10^{-7 (Sorensen *et al.* 1990) less effective 4-pregnen-20x-ol 3-one (10⁻⁷
to 10^{-9} M), 4-pregnen-20β-ol-3-one, dihydroxyprogesterol, and
androstendione (10^{-7} to 10^{-9} M); two ovulatory pheromones:
prostaglandin E₃ a to 10⁻⁹ M), 4-pregnen-20β-ol-3-one, dihydroxyprogesterol, and
androstendione $(10^{-7}$ to 10^{-9} M); two ovulatory pheromones:
prostaglandin F_{2a} and 15 ketoprostaglandin F_{2a} (PGF_{2a}, 15K-
PEC + 10^{-7} to 10^{-11} androstendione (10 $^{\circ}$ to 10 $^{\circ}$ M); two ovulatory pheromones
prostaglandin F_{2a} and 15 ketoprostaglandin F_{2a} (PGF_{2a}, 15K-
PFG_{2a}; 10⁻⁷ to 10⁻¹¹M); hypoxanthine-3(N)-oxide (10⁻⁷ to
10⁻¹³M), a probable to prostaglandin F_{2a} and 15 ketoprostaglandin F_{2a} (PGF_{2a}, 15K-
PFG_{2a}; 10⁻⁷ to 10⁻¹¹M); hypoxanthine-3(N)-oxide (10⁻⁷ to
10⁻¹³M), a probable alarm pheromone (Pfeiffer 1982), and
hypoxanthine (10⁻⁷ to 10 PFG_{2a} ; 10 $'$ to 10 $''$ M); hypoxanthine-3(N)-oxide (10 $'$ to 10⁻¹³M), a probable alarm pheromone (Pfeiffer 1982), and hypoxanthine (10⁻⁷ to 10⁻⁹M), which do not result in a record-
able EOG during epithelial app hypoxanthine $(10^{-7}$ to 10^{-9} M), which do not result in a recordable EOG during epithelial application (P.W. Sorensen, personal communication).

3. RESULTS AND DISCUSSION

The interstimulus activity is characterized by the higher and frequently burst-like activity of mitral cells The interstimulus activity is characterized by the higher and frequently burst-like activity of mitral cells (mean value 2.7 s^{-1}) driven by the spontaneously active enithelial receptor neurons. During pauses in the higher and frequently burst-like activity of mitral cells
(mean value 2.7s⁻¹) driven by the spontaneously active
epithelial receptor neurons. During pauses in the mitral
cell activity ruffed cell potentials (mean value (mean value 2.7 s⁻¹) driven by the spontaneously active
epithelial receptor neurons. During pauses in the mitral
cell activity, ruffed cell potentials (mean value 0.75 s⁻¹)
are present. During application of an inhibi epithelial receptor neurons. During pauses in the mitral cell activity, ruffed cell potentials (mean value 0.75 s^{-1}) are present. During application of an inhibitory olfactory cell activity, ruffed cell potentials (mean value 0.75 s⁻¹)
are present. During application of an inhibitory olfactory
stimulus the activity of receptor neurons is blocked and
the mitral cells are inhibited. Consequently are present. During application of an inhibitory olfactory
stimulus the activity of receptor neurons is blocked and
the mitral cells are inhibited. Consequently, lateral inhibi-
tion of ruffed cells via granule cells activ stimulus the activity of receptor neurons is blocked and
the mitral cells are inhibited. Consequently, lateral inhibi-
tion of ruffed cells via granule cells activated by mitral
cells is no longer present and results in a the mitral cells are inhibited. Consequently, lateral inhibition of ruffed cells via granule cells activated by mitral
cells is no longer present and results in a higher activity
of ruffed cells. During epithelial applicat tion of ruffed cells via granule cells activated by mitral
cells is no longer present and results in a higher activity
of ruffed cells. During epithelial application of an excita-
tory of actory stimulus increased activity cells is no longer present and results in a higher activity
of ruffed cells. During epithelial application of an excita-
tory olfactory stimulus, increased activity of receptor cells
results in excitation of mitral cells, of ruffed cells. During epithelial application of an excita-
tory olfactory stimulus, increased activity of receptor cells
results in excitation of mitral cells, which activate granule
cells, laterally, inhibiting, ruffed, tory olfactory stimulus, increased activity of receptor cells
results in excitation of mitral cells, which activate granule
cells. Iaterally. inhibiting ruffed cells. Figure 1 shows
responses of three mitral cells and one results in excitation of mitral cells, which activate granule
cells laterally inhibiting ruffed cells. Figure 1 shows
responses of three mitral cells and one ruffed cell during
application of hypoxanthine-3(N)-oxide and hy cells laterally inhibiting ruffed cells. Figure 1 shows
responses of three mitral cells and one ruffed cell during
application of hypoxanthine-3(N)-oxide and hypox-
anthine in different molarities. These stimuli do not res responses of three mitral cells and one ruffed cell during
application of hypoxanthine- $3(N)$ -oxide and hypox-
anthine in different molarities. These stimuli do not result
in a recordable EOG during epithelial application application of hypoxanthine-3(N)-oxide and hypox-
anthine in different molarities. These stimuli do not result
in a recordable EOG during epithelial application (P. W.
Sorensen, personal communication) Figure 1 presents a anthine in different molarities. These stimuli do not result
in a recordable EOG during epithelial application (P. W.
Sorensen, personal communication). Figure 1 presents a
simultaneous recording from three mitral cells an in a recordable EOG during epithelial application (P. W.
Sorensen, personal communication). Figure 1 presents a consimultaneous recording from three mitral cells and from a conservation of the probable alarm Sorensen, personal communication). Figure 1 presents a
simultaneous recording from three mitral cells and from
one ruffed cell. During application of the probable alarm
pheromone in the highest concentration $(10^{-7}M)$ an simultaneous recording from three mitral cells and from
one ruffed cell. During application of the probable alarm
pheromone in the highest concentration $(10^{-7} M)$, an
excitation is recorded from the three mitral cells an one ruffed cell. During application of the probable alarm
pheromone in the highest concentration $(10^{-7} M)$, and a excitation is recorded from the three mitral cells and a

total lateral inhibition from the ruffed cell. Concentratotal lateral inhibition from the ruffed cell. Concentra-
tions of 10^{-7} , 10^{-9} , 10^{-11} and 10^{-13} M excite mitral cells 1
and 2, and again the ruffed cell is totally inhibited total lateral inhibition from the ruffed cell. Concentra-
tions of 10^{-7} , 10^{-9} , 10^{-11} and 10^{-13} M excite mitral cells 1
and 2, and again the ruffed cell is totally inhibited.
Mitral cell 3 remains indifferent d tions of 10^{-7} , 10^{-9} , 10^{-11} and 10^{-13} M excite mitral cells 1
and 2, and again the ruffed cell is totally inhibited.
Mitral cell 3 remains indifferent during application of the
 10^{-9} and 10^{-11} molar concen and 2, and again the ruffed cell is totally inhibited.
Mitral cell 3 remains indifferent during application of the 10^{-9} and 10^{-11} molar concentrations and is slightly inhib-
ited during application of the 10^{-13} m Mitral cell 3 remains indifferent during application of the 10^{-9} and 10^{-11} molar concentrations and is slightly inhibited during application of the 10^{-13} molar concentration.
The major interaction between mitral 10^{-9} and 10^{-11} molar concentrations and is slightly inhibited during application of the 10^{-13} molar concentration.
The major interaction between mitral cell 2 and the ruffed cell can clearly be seen during applic ited during application of the 10^{-13} molar concentration.
The major interaction between mitral cell 2 and the
ruffed cell can clearly be seen during application of
hypoxanthine $(10^{-9} M)$; only mitral cell 2 is excited The major interaction between mitral cell 2 and the ruffed cell can clearly be seen during application of hypoxanthine $(10^{-9} M)$: only mitral cell 2 is excited and the ruffed cell is totally laterally inhibited ruffed cell can clearly be seen during a
hypoxanthine $(10^{-9} M)$: only mitral cell 2
the ruffed cell is totally laterally inhibited.
Contrasting interactions between mitr poxanthine $(10^{-9} M)$: only mitral cell 2 is excited and
e ruffed cell is totally laterally inhibited.
Contrasting interactions between mitral cells and
ffed cells were present that even in the lowest concen-

the ruffed cell is totally laterally inhibited.
Contrasting interactions between mitral cells and
ruffed cells were present that even in the lowest concen-
tration resulted in a drastic intensification of centrally Contrasting interactions between mitral cells and
ruffed cells were present that even in the lowest concen-
tration resulted in a drastic intensification of centrally
transmitted information. An inhibition was recorded ruffed cells were present that even in the lowest concentration resulted in a drastic intensification of centrally transmitted information. An inhibition was recorded more frequently from mitral cells and decreasing latera tration resulted in a drastic intensification of centrally
transmitted information. An inhibition was recorded
more frequently from mitral cells, and decreasing lateral
inhibition via granule cells resulted in an activatio transmitted information. An inhibition was recorded
more frequently from mitral cells, and decreasing lateral
inhibition via granule cells resulted in an activation of
ruffed cells Activation of ruffed cells resulted in an more frequently from mitral cells, and decreasing lateral
inhibition via granule cells resulted in an activation of
ruffed cells. Activation of ruffed cells resulted in an actiinhibition via granule cells resulted in an activation of ruffed cells. Activation of ruffed cells resulted in an activation of pools of granule cells laterally inhibiting pools of mitral cells in their vicinity. ruffed cells. Activation of ruffed
vation of pools of granule cells
of mitral cells in their vicinity.
In contrast to EOG recordin In tion of pools of granule cells laterally inhibiting pools

In contrast to EOG recording (Sorensen *et al.* 1990),

plication of bigbly effective and less effective preovula-

of mitral cells in their vicinity.
In contrast to EOG recording (Sorensen *et al.* 1990),
application of highly effective and less effective preovula-In contrast to EOG recording (Sorensen *et al.* 1990), application of highly effective and less effective preovulatory pheromone stimuli resulted in more similar responses recorded from olfactory bulb relay neurons application of highly effective and less effective preovulatory pheromone stimuli resulted in more similar responses recorded from olfactory bulb relay neurons.
The EOG is a slow (DC) potential change recorded in tory pheromone stimuli resulted in more similar
responses recorded from olfactory bulb relay neurons.
The EOG is a slow (DC) potential change recorded in
teleosts from the water above the surface of the olfactory responses recorded from olfactory bulb relay neurons.
The EOG is a slow (DC) potential change recorded in
teleosts from the water above the surface of the olfactory The EOG is a slow (DC) potential change recorded in teleosts from the water above the surface of the olfactory organ in response to chemical stimulation and is suggested to be the population average of receptor potential teleosts from the water above the surface of the olfactory
organ in response to chemical stimulation and is
suggested to be the population average of receptor poten-
tials responsible for the initiation of neural impulses organ in response to chemical stimulation and is
suggested to be the population average of receptor poten-
tials responsible for the initiation of neural impulses.
From the present recordings from olfactory bulb relay suggested to be the population average of receptor potentials responsible for the initiation of neural impulses. tials responsible for the initiation of neural impulses.
From the present recordings from olfactory bulb relay
neurons, however, the EOG obviously is not a reliable
indicator of olfactory organ sensitivity and specificity From the present recordings from olfactory bulb relay
neurons, however, the EOG obviously is not a reliable
indicator of olfactory organ sensitivity and specificity to
odorants in fishes neurons, however, the EOG obviously is not a reliable indicator of olfactory organ sensitivity and specificity to odorants in fishes. dicator of olfactory organ sensitivity and specificity to
orants in fishes.
Olfactory bulb relay neurons frequently respond to a
mnaratively great number of olfactory stimuli: amino

odorants in fishes.
Colfactory bulb relay neurons frequently respond to a
comparatively great number of olfactory stimuli: amino
acide prequalatory and qualatory stimuli (figure 2), and Olfactory bulb relay neurons frequently respond to a
comparatively great number of olfactory stimuli: amino
acids, preovulatory and ovulatory stimuli (figure 2), and
contrasting interactions between mitral cells and ruffed comparatively great number of olfactory stimuli: amino
acids, preovulatory and ovulatory stimuli (figure 2), and
contrasting interactions between mitral cells and ruffed
cells were recorded frequently during stimulus appli acids, preovulatory and ovulatory stimuli (figure 2), and
contrasting interactions between mitral cells and ruffed
cells were recorded frequently during stimulus applica-
tion (figure 1). However, significant differences i tion (contrasting interactions between mitral cells and ruffed
cells were recorded frequently during stimulus applica-
tion (figure 1). However, significant differences in the

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excitation; 0, indifference; $-$, inhibition.
effectiveness, which are obvious in the EOG during appli-Figure 2. Summary of responses recorded from (*a*) 81 mitral cells and (*b*) 68 ruffed cells. Alarm pheromone (a.p.) is
hypoxanthine-3(N)-oxide: alarm pheromone control is hypoxanthine: 17–208 is prequulatory pheromone 17 Figure 2. Summary of responses recorded from (*a*) 81 mitral cells and (*b*) 68 ruffed cells. Alarm pheromone (a.
hypoxanthine-3(N)-oxide; alarm pheromone control is hypoxanthine; 17, 20β is preovulatory pheromone 17,
20ß hypoxanthine-3(N)-oxide; alarm pheromone control is hypoxanthine; 17, 20 β is preovulatory pheromone 17,
20 β -dihydroxyprogesterone; PGF_{2a} is ovulatory pheromone prostaglandine F_{2a}; stimulus concentration is 10⁻⁹

effectiveness, which are obvious in the EOG during application of different stimuli, were not present in recordings from olfactory bulb relay neurons effectiveness, which are obvious in the cation of different stimuli, were not from olfactory bulb relay neurons.
The fish alarm pheromone system tion of different stimuli, were not present in recordings
om olfactory bulb relay neurons.
The fish alarm pheromone system is characterized by
stinctive enidermal club cells that contain the alarm

from olfactory bulb relay neurons. a
The fish alarm pheromone system is characterized by
distinctive epidermal club cells that contain the alarm are
pheromone probably hypoxanthine-3(N)-oxide In The fish alarm pheromone system is characterized by
distinctive epidermal club cells that contain the alarm
pheromone, probably hypoxanthine- $3(N)$ -oxide. In
contrast to EOG recordings application of the probable distinctive epidermal club cells that contain the alarm
pheromone, probably hypoxanthine-3(N)-oxide. In
contrast to EOG recordings, application of the probable
alarm pheromone resulted in a similar effectiveness to pheromone, probably hypoxanthine- $3(N)$ -oxide. In contrast to EOG recordings, application of the probable alarm pheromone resulted in a similar effectiveness to that of the preovulatory and the ovulatory pheromones contrast to EOG recordings, application of the probable
alarm pheromone resulted in a similar effectiveness to
that of the preovulatory and the ovulatory pheromones,
and the amino acid (figure 2). In summary natural alarm pheromone resulted in a similar effectiveness to
that of the preovulatory and the ovulatory pheromones,
and the amino acid (figure 2). In summary, natural
important stimuli are excellently discriminated by that of the preovulatory and the ovulatory pheromones,
and the amino acid (figure 2). In summary, natural
important stimuli are excellently discriminated by
individual mitral and ruffed cells. During application of and the amino acid (figure 2). In summary, natural
important stimuli are excellently discriminated by
individual mitral and ruffed cells. During application of
non-familiar stimuli responses are slightly more similar important stimuli are excellently discriminated by individual mitral and ruffed cells. During application of non-familiar stimuli, responses are slightly more similar, individual mitral and ruffed cells. During application of
non-familiar stimuli, responses are slightly more similar,
i.e. less discriminative. Contrasting interactions between
mitral cells and ruffed cells were found frequ non-familiar stimuli, responses are slightly more similar,
i.e. less discriminative. Contrasting interactions between
mitral cells and ruffed cells were found frequently during
simultaneous recordings. Details were recentl i.e. less discriminative. Contrasting interactions between
mitral cells and ruffed cells were found frequently during
simultaneous recordings. Details were recently published
(Zinnel et al. 1999–2000). Dose-dependent decli mitral cells and ruffed cells were found frequently during
simultaneous recordings. Details were recently published
(Zippel *et al.* 1999, 2000). Dose-dependent declining simultaneous recordings. Details were recently published (Zippel *et al.* 1999, 2000). Dose-dependent declining excitatory or inhibitory responses were only apparent in $40-45\%$ of recordings In 25% lowering the stimu (Zippel *et al.* 1999, 2000). Dose-dependent declining excitatory or inhibitory responses were only apparent in $40-45\%$ of recordings. In 25%, lowering the stimulus concentration resulted in increasing excitation or inh excitatory or inhibitory responses were only apparent in $40-45\%$ of recordings. In 25% , lowering the stimulus concentration resulted in increasing excitation or inhibition. In 30% of cells indifferent responses an 40–45% of recordings. In 25%, lowering the stimulus this issue) result from stimulus-specific cells somewhere concentration resulted in increasing excitation or inhibi-
in the olfactory bulb projecting to the respective t reversible response patterns, were recorded. Responses tion. In 30% of cells indifferent responses, and in 5% reversible response patterns, were recorded. Responses from mitral cells were more frequently inhibitions, and those from ruffed cells excitations. The dominanc reversible response patterns, were recorded. Responses
from mitral cells were more frequently inhibitions, and
those from ruffed cells excitations. The dominance of
mitral cell inhibition was high during non-familiar from mitral cells were more frequently inhibitions, and
those from ruffed cells excitations. The dominance of
mitral cell inhibition was high during non-familiar
stimulus application and less during application of biothose from ruffed cells excitations. The dominance of mitral cell inhibition was high during non-familiar stimulus application, and less during application of bio-logically relevant stimuli. Details however of response mitral cell inhibition was high during non-familiar
stimulus application, and less during application of bio-
logically relevant stimuli. Details, however, of response
characteristics warrant further investigation. Indiffe stimulus application, and less during application of biologically relevant stimuli. Details, however, of response characteristics warrant further investigation. Indifferent logically relevant stimuli. Details, however, of response
characteristics warrant further investigation. Indifferent
neurons are either specialized for application of different
stimuli or like relay neurons in the rat (Ez characteristics warrant further investigation. Indifferent
neurons are either specialized for application of different
stimuli, or, like relay neurons in the rat (Ezeh *et al.* 1993),
in which electrical stimulation of the neurons are either specialized for application of different
stimuli, or, like relay neurons in the rat (Ezeh *et al.* 1993),
in which electrical stimulation of the olfactory nerve
results in no effect during intracellular stimuli, or, like relay neurons in the rat (Ezeh *et al.* 1993), in which electrical stimulation of the olfactory nerve results in no effect during intracellular recording, are not in which electrical stimulation of the olfactory nerve
results in no effect during intracellular recording, are not
responsible for olfactory stimuli. Information processing
in the goldfish elfactory bulb offers some obvio results in no effect during intracellular recording, are not
responsible for olfactory stimuli. Information processing
in the goldfish olfactory bulb offers some obvious simi-
larities to the visual system: mitral and ruff responsible for olfactory stimuli. Information processing
in the goldfish olfactory bulb offers some obvious simi-
larities to the visual system: mitral and ruffed cells' *Phil. Trans. R. Soc. Lond.* B (2000)

interstimulus and stimulus interaction reminds one of
'on- and off-centre' ganglion cells in the retina however interstimulus and stimulus interaction reminds one of

'on- and off-centre' ganglion cells in the retina, however,

also like cortical complex neurons that heavily depend on 'on- and off-centre' ganglion cells in the retina, however, also like cortical complex neurons that heavily depend on 'on- and off-centre' ganglion cells in the retina, however,
also like cortical complex neurons that heavily depend on
the 'shape' of the stimulus applied in the retina. That is,
an excitatory stimulus turns the mitral cell also like cortical complex neurons that heavily depend on
the 'shape' of the stimulus applied in the retina. That is,
an excitatory stimulus turns the mitral cell on and the
ruffed cell off and an inhibitory stimulus turns the 'shape' of the stimulus applied in the retina. That is,
an excitatory stimulus turns the mitral cell on and the
ruffed cell off, and an inhibitory stimulus turns the mitral
cell off and releases the activity of the res an excitatory stimulus turns the mitral cell on and the ruffed cell off, and an inhibitory stimulus turns the mitral cell off and releases the activity of the respective ruffed cell. Therefore mitral cells (and ruffed cell ruffed cell off, and an inhibitory stimulus turns the mitral cell off and releases the activity of the respective ruffed
cell. Therefore mitral cells (and ruffed cells) can become
'on- and off-centre' neurons as well, or remain indifferent
denending on the stimulus annlied cell. Therefore mitral cells (and ruff

'on- and off-centre' neurons as well,

depending on the stimulus applied.

In the three series of experiments In the off-centre' neurons as well, or remain indifferent
pending on the stimulus applied.
In the three series of experiments in which recordings
ree made from a total of approximately 180 mitral cells

depending on the stimulus applied.
In the three series of experiments in which recordings
were made from a total of approximately 180 mitral cells
and 90 ruffed cells we were not able to determine a In the three series of experiments in which recordings
were made from a total of approximately 180 mitral cells
and 90 ruffed cells we were not able to determine a
"enecific" bulbar area (neither lateral or medial nor were made from a total of approximately 180 mitral cells
and 90 ruffed cells we were not able to determine a
'specific' bulbar area (neither lateral or medial nor
rostral or caudal) to which any of the non-familiar or and 90 ruffed cells we were not able to determine a

'specific' bulbar area (neither lateral or medial nor

rostral or caudal) to which any of the non-familiar or

pheromone stimuli was preferentially projected 'specific' bulbar area (neither lateral or medial nor
rostral or caudal) to which any of the non-familiar or
pheromone stimuli was preferentially projected.
Hypothetically behavioural specificities recorded rostral or caudal) to which any of the non-familiar or
pheromone stimuli was preferentially projected.
Hypothetically, behavioural specificities recorded pheromone stimuli was preferentially projected.
Hypothetically, behavioural specificities recorded
following dissection of different subtracts (see Zippel,
this issue) result from stimulus-specific cells somewhere Hypothetically, behavioural specificities recorded
following dissection of different subtracts (see Zippel,
this issue) result from stimulus-specific cells somewhere
in the olfactory bulb projecting to the respective telen following dissection of different subtracts (see Zippel,
this issue) result from stimulus-specific cells somewhere
in the olfactory bulb projecting to the respective telence-
phalic nuclei via different subtracts (see Zip this issue) result from stimulus-specific cells somewhere value is via different subtracts (see Zippel *et al.* 000) for details).
In contrast to EOG recordings, in which the impor-
nee of an olfactory stimulus at least partly results in

(2000) for details).
In contrast to EOG recordings, in which the importance of an olfactory stimulus at least partly results in
significantly different amplitudes (Sorensen *et al.* 1990). In contrast to EOG recordings, in which the importance of an olfactory stimulus at least partly results in significantly different amplitudes (Sorensen *et al.* 1990), a similar image cannot be recorded from olfactory bulb tance of an olfactory stimulus at least partly results in significantly different amplitudes (Sorensen *et al.* 1990), a similar image cannot be recorded from olfactory bulb relay neurons. The present study does not conta significantly different amplitudes (Sorensen *et al.* 1990), a similar image cannot be recorded from olfactory bulb relay neurons. The present study does not contain original FOC data because a number of stimuli (the two similar image cannot be recorded from olfactory bulb
relay neurons. The present study does not contain original
EOG data because a number of stimuli (the two purines relay neurons. The present study does not contain original
EOG data because a number of stimuli (the two purines
and hydrocortisone) do not result in a recordable EOG in
any concentration (P W Sorensen, personal communica-EOG data because a number of stimuli (the two purines
and hydrocortisone) do not result in a recordable EOG in
any concentration (P. W. Sorensen, personal communica-
tion) and the rest of the stimuli were annlied in low and hydrocortisone) do not result in a recordable EOG in
any concentration (P. W. Sorensen, personal communica-
tion), and the rest of the stimuli were applied in low
concentrations, which do not result in a recordable EOG any concentration (P. W. Sorensen, personal communication), and the rest of the stimuli were applied in low concentrations, which do not result in a recordable EOG tion), and the rest of the stimuli were applied in low
concentrations, which do not result in a recordable EOG
either. Significantly different EOG amplitudes recorded
at high $(10^{-3} \tcdot 10^{-4} \text{ M})$ concentrations of amino concentrations, which do not result in a recordable EOG
either. Significantly different EOG amplitudes recorded
at high $(10^{-3}, 10^{-4} M)$ concentrations of amino acids,
and after axotomy when the number of recentor neurons either. Significantly different EOG amplitudes recorded
at high $(10^{-3}, 10^{-4} M)$ concentrations of amino acids,
and after axotomy, when the number of receptor neurons

is at a minimum (Zippel *et al.* 1997), are obviously
artefacts because lower $(10^{-5} \t 10^{-6} \text{ M})$ concentrations is at a minimum (Zippel *et al.* 1997), are obviously artefacts, because lower $(10^{-5}, 10^{-6} \text{ M})$ concentrations result in similar EOG amplitudes and below 10^{-6} molar is at a minimum (Zippel *et al.* 1997), are obviously
artefacts, because lower $(10^{-5}, 10^{-6} \text{ M})$ concentrations
result in similar EOG amplitudes, and below 10^{-6} molar
concentrations do not result in a recordable EOG artefacts, because lower $(10^{-5}, 10^{-6} \text{ M})$ concentrations
result in similar EOG amplitudes, and below 10^{-6} molar
concentrations do not result in a recordable EOG (Zippel result in similar EOG amplitudes, and below 10⁻⁶ molar concentrations do not result in a recordable EOG (Zippel *et al.* 1997). The present recordings from olfactory bulb mitral and ruffed cells clearly indicate that man concentrations do not result in a recordable EOG (Zippel
et al. 1997). The present recordings from olfactory bulb
mitral and ruffed cells clearly indicate that many (and in
the EOG highly effective and totally ineffective) *et al.* 1997). The present recordings from olfactory bulb mitral and ruffed cells clearly indicate that many (and in the EOG highly effective and totally ineffective) stimuli in general elicit rather similar amounts of ac mitral and ruffed cells clearly indicate that many (and in
the EOG highly effective and totally ineffective) stimuli
in general elicit rather similar amounts of activation, the EOG highly effective and totally ineffective) stimuli
in general elicit rather similar amounts of activation,
depression or indifferent responses. In different relay
neurons however responses to different stimuli can v in general elicit rather similar amounts of activation,
depression or indifferent responses. In different relay
neurons, however, responses to different stimuli can vary
drastically i.e. stimuli are excellently discriminat depression or indifferent responses. In different relay
neurons, however, responses to different stimuli can vary
drastically, i.e. stimuli are excellently discriminated by
individual relay neurons. The pheromonal or learn neurons, however, responses to different stimuli can vary
drastically, i.e. stimuli are excellently discriminated by
individual relay neurons. The pheromonal or learned-by-
experience importance of a stimulus probably is n drastically, i.e. stimuli are excellently discriminated by
individual relay neurons. The pheromonal or learned-by-
experience importance of a stimulus probably is not
detected by enithelial sensors but by central (telencep individual relay neurons. The pheromonal or learned-by-
experience importance of a stimulus probably is not
detected by epithelial sensors but by central (telencephalic)
nuclei as in other sensory modalities experience importance of a stimulus probably is not detected by epithelial sensors but by central (telencephalic) nuclei, as in other sensory modalities.

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distinctive initial unmyelinated portion of the axon in the
olfactory bulb of the goldfish *(Carassius auratus*) II. Fine strucdistinctive initial unmyelinated portion of the axon in the olfactory bulb of the goldfish *(Carassius auratus*). II. Fine structure of the ruffed cell. *J. Comp. Neurol*. **193**, 119-145. olfactorybulb of the goldfish (*Carassius auratus*). II. Fine structure of the ruffed cell. \tilde{J} . *Comp. Neurol*. **193**, 119–145.
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the olfactory bulb of the goldfish *(Ca* osaka, T. & Hama, K. 1979 Ruffed cell: a new type of neuron
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impregnation and serial thin sec with a distinctive initial unmyelinated portion of the axon in the olfactory bulb of the goldfish *(Carassius auratus)*. I. Golgi [impregnation and s](http://pippo.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0021-9967^28^29186L.301[aid=536170,nlm=457934])erial thin sectioning studies. *[J. Comp.](http://pippo.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0021-9967^28^29186L.301[aid=536170,nlm=457934]) Neurol.* **¹⁸⁶**, 301^320.
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