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Solitary chemosensory cells – taste, common chemical sense or what?

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Introduction

The skin surface of most fishes is not keratinized. The mucus-covered cell surface membranes are directly exposed to water, which is an excellent solvent and carrier for a wide variety of substances (Atema, 1988; Carr, 1988). No wonder that fish skin hosts abundant chemosensory structures, such as taste buds, free nerve endings, and **solitary chemosensory cells**. Ever since Leydig (1851), taste buds have been a focal point of scientific attention, but solitary chemosensory cells only to a much lesser degree. It is the aim of the present review to summarize knowledge on distribution, morphology and function of solitary chemosensory cell systems. Fine structure is deliberately spared, as this aspect is covered by a recent review article by Whitear (in press).

Solitary chemosensory cells (SSCs) are vertebrate secondary epidermal sensory cells, which resemble taste bud (TB) receptors (Whitear, 1965). In the recent literature these 'putative chemoreceptors' (Lane and Whitear, 1982) are also called 'scattered chemosensory cells' (Bullock and Roberts, 1974; Whitear, 1952, 1971) or 'isolated chemosensory cells'; it is however preferable not to use the last term because it may foster confusion with dissociated taste bud cells (Kinnamon *et al.*, 1988).

Because of their structural resemblance to actinopterygian SCCs, the lamprey 'oligovillous cells' (Whitear and Lane, 1983) and frog tadpole 'Stiftchenzellen' (Whitear, 1976) are included in the present review; for a review of the older literature on these cell types see these papers and Whitear (1971). The term SCCs is used here for all these cell types; arbitrarily, SCCs are defined as secondary chemosensory cells, embedded within generalized epidermis, with one or a few apical microvilli and synaptic contacts to primary afferent nerve fibres.

Spindle-shaped, presumed sensory cells were described by Kölliker (1886) in the tadpole skin and by Morrill (1895) in the epidermis of free pectoral fin rays of Triglidae (Fig. 1, sea robins or gurnards), and occasionally reappeared in the literature (e.g. Bannister, 1965; Dawson, 1934; Schulte and Holl, 1972; for reviews of the older literature see Lane, 1977; Whitear, 1952, 1971, in press). Fine structural investigations (Whitear, 1965, 1971) revealed the similarity of these cells to TB receptors and showed their association with nerve fibres, SCCs were thus proposed to be chemosensory.

SCCs were found in a variety of actinopterygian fishes (Lane and Whitear, 1982; Reutter, 1986; Whitear, 1971) including sturgeons, lungfish (Whitear, in press), but also in lampreys (Whitear and Lane, 1983) and in ranid tadpoles (Kölliker, 1886; Whitear, 1976). In most species SCCs are scattered over the body surface (Fig. 2), including the oral cavity (Sibbing and Uribe, 1985; Whitear, 1971). Owing to their widespread occurrence, probably in more than half of all vertebrade species, and their abundance (Kotrschal, in press), SCCs may be regarded as a major class of vertebrate chemosensory cells.

However, no functional information is available on such generalized SCC systems. This is due to the small size of teleost SCCs, their scattered distribution and a plexiform innervation (Whitear, 1952), mingling with fibres passing to TBs and free nerve endings.

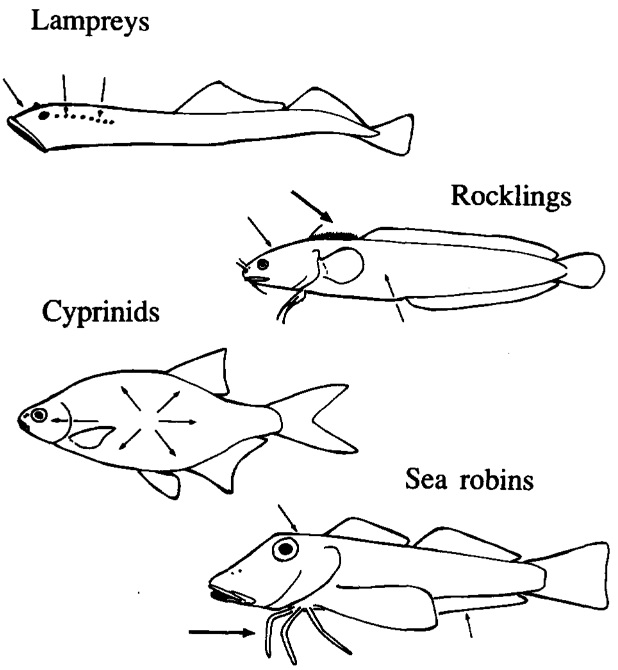


Fig.1. Lampreys, rocklings, cyprinids and sea robins were recently utilized models in solitary chemosensory cell (SCC) research. Bold arrows point at locations where SCCs are aggregated: the anterior dorsal fin in rocklings and the free pectoral fin rays in sea robins. In the cyprinids, as in most fish including those mentioned above, SCCs are evenly spread over the body surface (light arrows; comp. Fig. 4).

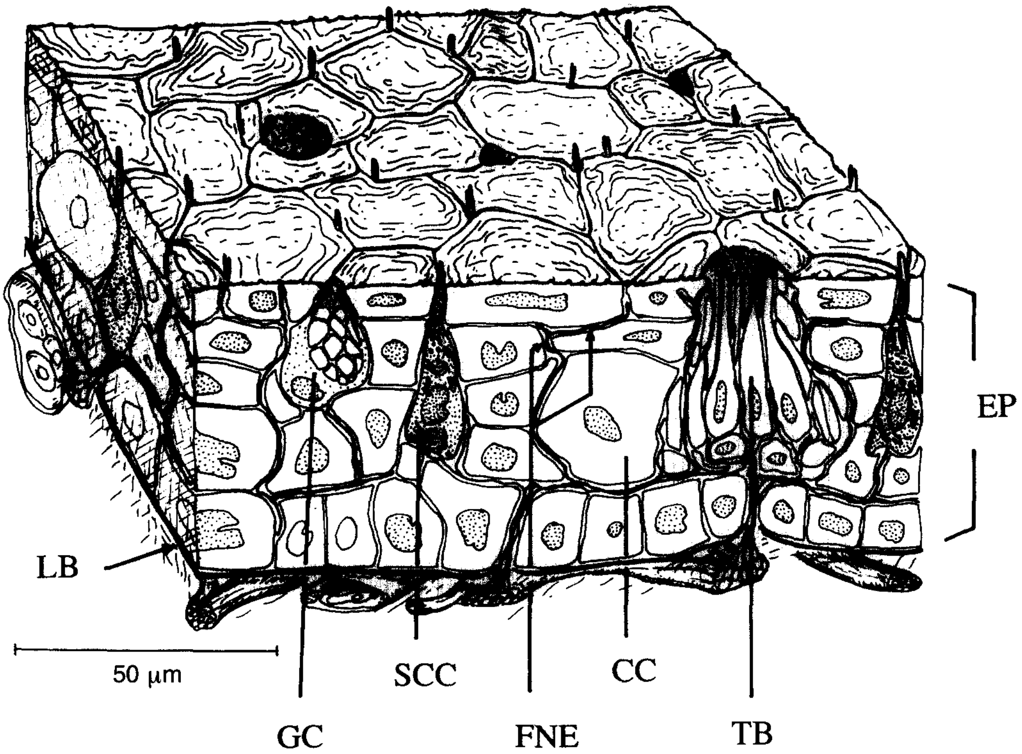


Fig. 2. Diagram of a generalized, scattered, solitary chemosensory cell (SCC) arrangement; unscaled cyprinid forehead skin. Taste bud (TB) pores, SCC apices and openings of goblet cells (GC) protrude between the squamous epidermal cells. The epidermis (EP) contains SCCs, TBs, glandular cells such as goblet and club cells (CC) and unspecialized epidermal cells. Ionocytes and Merkel cells are present but not shown. A subepidermal nerve plexus feeds fibres into the epidermis, which synapse with epidermal sensory cells or branch into free nerve endings (FNE). LB, lamina basalis. SCC density is approximately 1000–4000 per mm^2.

Therefore, selective elimination and behavioural experiments, as well as nerve tracing, were not feasible using conventional methods. Clearly, fish were needed that carry SCCs and their innervation in a more concentrated arrangement and therefore facilitate specific investigations (Fig. 1).

Such favourable conditions were met in the case of lamprey SCCs (= oligovillous cells; Baatrup, 1983 a,b, 1985; Whitear and Lane, 1983), but they had no TB-like terminal buds. Suction-electrode recordings by Baatrup and Doving (1985) provided the first direct evidence that these SCC-like cells were indeed chemosensory and that their responses differed from those of the lamprey TB analogues (Baatrup, 1984 a,b, 1985; Baatrup and Doving, 1985).

Sea robins' pectoral fin rays are another favourable model (Fig. 1). By means of their finger-like free rays, these benthic fishes probe the substrate for food. These rays do not contain taste buds, but papillae ('claviform bodies', d'Evant, 1903) with SCCs and free nerve endings (Morrill, 1895; Scharrer, 1935; Whitear, 1971). The innervation of these rays seems exclusively spinal; their central sensory representations cause distinct swellings within the rostrodorsal spinal cord (Morrill, 1895; Finger, 1982). Chemosensory responses from these pectoral fin ray nerves do not match those from the olfactory or from the taste system (Silver and Finger, 1984).

A suitable model for the exploration of SCC function in teleost fishes was described by Kotrschal *et al.* (1984, 1985). The specialized anterior dorsal fin (ADF) of rocklings (e.g. *Gaidropsarus* and *Ciliata*, Gadidae, Fig. 1) carries millions of SCCs, but no other epidermal chemosensory cells (Fig. 3). Nerve tracing (Kotrschal and Whitear, 1988) and denervation experiments (Whitear and Kotrschal, 1988) established the facial innervation of these ADF-SCCs. Electrophysiology in this system revealed the first functional data on actinopterygian SCCs (Peters *et al.*, 1987, 1989, 1991) and showed that these SCCs respond mainly to heterospecific fish mucus. Behavioural evidence supports these results (Kotrschal *etal.*, 1989).

How solitary chemosensory cell (SCC) systems are arranged

A generalized, scattered distribution of SCCs over the body surface was found in most fish, in lampreys (Whitear and Lane, 1983) and in frog tadpoles (Kölliker, 1886; Meyer, 1962; Whitear, 1976). SCCs are embedded between unspecialized epidermal cells, often

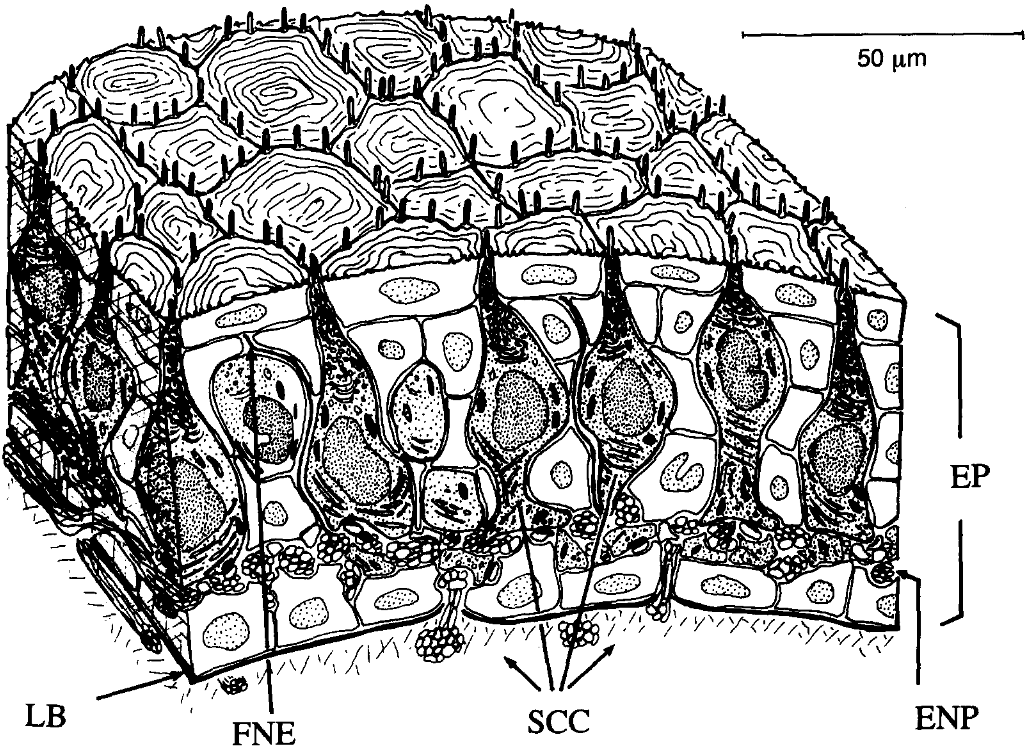


Fig. 3. Diagram of the specialized, aggregated assemblage of solitary chemosensory cells (SCC) in the fin ray epidermis (EP) of the rockling anterior dorsal fin. SCCs are the only epidermal chemosensory cells; there are no glandular cells. The prominent epidermal nerve plexus (ENP) consists mainly of facial fibres which synapse with the SCC bases. Spinal fibres contribute free nerve endings (FNE). LB, lamina basalis. SCC density is approximately 100 000 per mm^2.

interspersed with TBs and free neuromasts (Fig. 2). Epidermal glandular cells may be close, but do not contact SCCs. Their innervation is plexiform (Whitear, 1952); it is not known whether in the generalized system of scattered SCCs certain primary afferent nerves serve only SCCs, or whether fibres of the same nerve innervate both SCCs and TBs (but compare the rockling model). Also, the source of innervation – general cutaneous (spinal and trigeminal) or special visceral (facial) nerves, or both – is still unclear.

The rockling anterior dorsal fin (ADF) is an example of a specialized SCC arrangement (Figs 1 and 3). SCCs are tightly packed (Kotrschal *et al.*, 1984, 1985), but in most cases (Kotrschal *et al.*, 1990) are separated from each other by sheets of epidermal cells. Goblet cells or other glandular cells are lacking in the sensory-cell-loaded epidermis of the rockling ADF, where approximately 15% of the epidermal cells by number, and 30% by volume, are SCCs (Kotrschal *et al.*, 1990). The intra-epidermal nerve plexus consists mainly of extensively branching fibres of the recurrent facial nerve, which synapse with the SCC bases (Kotrschal and Whitear, 1988; Whitear and Kotrschal, 1988).

Distribution of SCCs among vertebrates

Figure 4 shows the known distribution of SCCs. Widespread as it is, it may not reflect the maximum SCC range within the vertebrates. Schreiner (1918) might have seen SCCs in hagfish, but there is no electron microscopical confirmation. A preliminary search for SCCs in the oral and branchial cavities of elasmobranchs was without success (Kotrschal, unpublished).

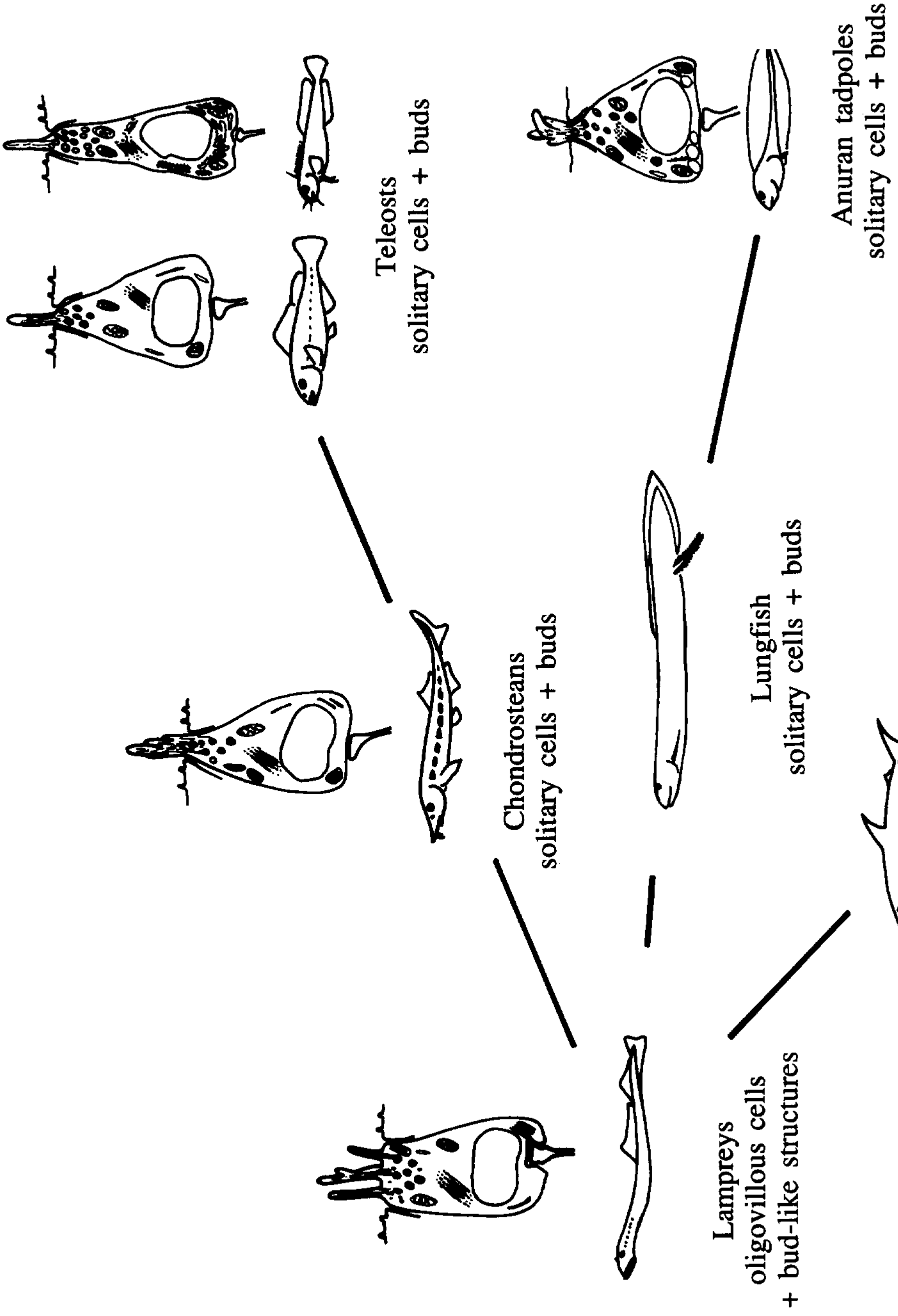
The cephalochordate *Branchiostoma* shows solitary receptor cells, discussed as chemo- and mechanoreceptors (Baatrup, 1981; Bone and Best, 1978; Franz, 1923). As these cells may be primary sensory (but see Schulte and Riehl, 1977) and have ciliated apices, they do not match the present definition of SCCs.

In the amphibians, SCC distribution may be more widespread than is currently known, but there are obstacles to quick surveys. A keratinized slough covers their epidermal surface and prohibits easy access by scanning electron microscopy; also, possible differences in methylene blue affinity of SCCs and skin pigmentation in different species may impair a survey for SCCs in aquatic amphibians; a good deal of tedious histology has been done with negative results (Whitear, personal communication, 1990).

If SCCs have phylogenetically 'survived' at all in the land tetrapods, the most promising skin areas are permanently moist surfaces of ectodermal origin, such as those found in the nasal and oral cavities. However, a recent search was without success (Whitear, pers. comm, 1990).

No matter what the SCC distribution outside the actinopterygian fish may be, SCCs have been found in many representatives of the latter, from sturgeons to perciforms (Fox *et al.*, 1980; Whitear, in press). Although in a few fish examined thoroughly (e.g. *Agonus cataphractus*, Whitear and Mittal, 1986) SCCs have not been seen, SCCs can be regarded as a major actinopterygian chemosensory system (see below).

There is some variation of SCC apex structure over the vertebrate pedigree (Fig. 4). This suggests a phylogenetic change from a few microvilli at the agnathan level of organization, which eventually merge or were replaced by a single villus at the agnathan–gnathostome transition. From the lower actinopterygians into the teleosts, this single villus may be branched and form a multiple tip. In the most modern, perciform teleosts,


Lampreys
oligovillous cells
+ bud-like structures
Elasmobranchs
? + buds
Chondrosteans
solitary cells + buds
Lungfish
solitary cells + buds
Teleosts
solitary cells + buds
Anuran tadpoles
solitary cells + buds

as well as in rocklings, the receptive villus is unbranched and shows a single tip only (Connes *et al.*, 1988; Kotrschal *et al.*, 1984; Schulte and Holl, 1972; Whitear, in press).

Distribution and abundance of SCCs and taste buds

A recent survey revealed data on distribution and abundance of the generalized, scattered SCC system in 12 species of teleosts (Kotrschal, in press).

SCCs are relatively evenly spread over the body surface, with densities being slightly higher in the dorsal areas. In most fish, however, external TBs are concentrated at focal points involved in food search, such as the lips, barbels, the pectoral and pelvic fins and along the ventral aspect of the head (Bardach and Atema, 1971; Gomahr *et al.* 1988; in press; Kiyohara *et al.*, 1980). Catfish show a more even distribution of TBs along the body surface (Atema, 1971), but densities may increase towards the rostral and ventral. The absence of any correlation between TB and SCC distribution may indicate different functions of the two systems (Kotrschal, in press). Whereas the interspecific variability of external TB density correlates with differences in lifestyles of species (Gomahr *et al.*, in press), no such correlation appears to exist with SCC density.

Consistently, approximately twice the average densities of SCCs were found in 100–200 μm diameter circular areas around free neuromasts (Kotrschal, in press). The functional significance of this pattern is unknown.

Among cyprinids, highest average densities of up to 4000 SCCs per mm^2 of skin were found in the roach *Rutilus rutilus.* In other European cyprinids examined (*Abramis ballerus, Alburnus alburnus, Chondrostoma nasus, Leuciscus cephalus, Phoxinus phoxinus, Scardinius erythrophthalmus*) densities were close to 2000 per mm^2. In pike-perch (*Lucioperca lucioperca*), a cichlid (*Haplochromis burtoni*) and two catfish species (*Ameiurus nebulosus, Clarias batrachus*), densities ranged between 1000 and 2000 per mm^2. Lowest densities, of 250 SCCs per mm^2, were found in the neon tetra (*Hyphessobrycon innesi*) (Kotrschal, in press). In the anterior dorsal fin rays of rocklings, where SCCs form a specialized chemosensory organ (Fig. 1, see below), SCC densities may approach 100000 per mm^2 (Fig. 3; Kotrschal *et al.*, 1984, 1985). Even in the cases of unspecialized, scattered SCC systems, there may be millions of SCCs spread over the entire body surface of individuals. In the seven species of cyprinids examined, total SCC numbers were always higher than those for TB sensory cells; SCCs account for 60–90% of all epidermal chemosensory cells. These numbers emphasize the functional importance of the SCC system. No data are available on the ontogenetic development and changes of SCC densities during growth.

The rockling model

The anterior dorsal fin (ADF) of rocklings (Gadidae, Telostei, e.g. genus *Gaidropsarus* and *Ciliata*) consists of 60–80 tiny fin rays, connected only at their bases with a fin membrane (Kotrschal *et al.*, 1984; Fig. 1). Fin rays perform a high-frequency, flagellum-

Fig. 4. Occurrence of solitary chemosensory cells (SCCs) over the vertebrate pedigree, from lampreys to teleosts and amphibians. Although gnathostome vertebrates may not have originated from lampreys, the figure suggests the direction of morphological change in SCC apex structure in the course of vertebrate evolution. In the elasmobranchs no SCCS have been found so far.

like, lateral movement (10–20 Hz, Peters *et al.*, 1989, 1991), which is coordinated into a sine-wave running rostro-caudally. In the resting fish, a few seconds of ADF undulation alternate with a few seconds of inactivity (Whitear and Kotrschal, 1988). Although the fin is always active before the fish starts swimming, it is too small for propulsion or steering of the swimming fish. Instead, water from its immediate surroundings is drawn into the fin and transported at velocities of up to 1 m s^{-1} through the ADF centre (Kotrschal *et al.*, unpubl.).

The ADF rays receive a considerable portion of the dorsal recurrent facial nerve fibres (Kotrschal *et al.*, 1984, 1985; Kotrschal and Whitear, 1988), which synapse with millions of SCCs, present in high densities in the epidermis of the ADF rays (Fig. 3; Kotrschal *et al.*, 1984, 1985). We therefore proposed that the ADF was a specialized sensory organ. Based on its innervation, Couch as early as 1864 suggested a sensory function for the ADF. Interpretations of the ADF that it acts as a lure attracting prey (Bogoljubsky, 1908) or as a water pump supplying TBs at the flank with stimulus-loaded water (Thomson, 1912) are rejected in the light of our recent findings.

Despite the presence of spinal nerve fibres, the ADF-SCCs synapse with fine-calibre primary afferent fibres of the recurrent facial nerve (Whitear and Kotrschal, 1988), which terminate exclusively in a peculiar, dorsal portion of the facial lobe (Kotrschal and Whitear, 1988); the ventral facial lobe receives mainly TB and tactile afferents (Peters *et al.*, 1991). Tracings with the carbocyanine dye DiI (Kotrschal and Finger, unpubl.) show that dorsal and ventral facial lobes have similar secondary projections, though those of the dorsal (SCC) facial lobe (where SCC afferents terminate) are more restricted.

Based on its facial innervation, we initially hypothesized (Kotrschal *et al.*, 1984, 1985; Whitear and Kotrschal, 1988) that the ADF was an additional food-detecting device in the crepuscular and nocturnally active rocklings. However, removal of the ADF had no effect on the ability of fish to find prey (Whitear and Kotrschal, 1988).

To our surprise, sum potential recordings from the afferent facial nerve fibres (Peters *et al.*, 1987, 1989, 1991) showed that the ADF-SCCs are narrowly tuned, heterospecific fish mucus detectors. No responses could be recorded from the ADF when mucus or body extracts (such as urinary bladder contents) of the same species were used, independent of the sex of the specimen from which we recorded, or the stimulus donor. Individuals were sexually mature and in pre-spawning condition. A function of the ADF in pheromone detection is therefore unlikely.

There was very little overlap in active stimulus spectrum with pelvic fin taste buds (Peters *et al.*, 1989, in press), which responded to a variety of classical taste stimuli, such as amino acids and extracts from prey animals. Tactile responses could be recorded from the facial fibres innervating the flanks of the rockling, but never from the ADF (Peters *et al.*, 1987 in press). It can be shown behaviourally that the ADF ray surface is touch-responsive (Whitear and Kotrschal, 1988); the ADF tactile sensitivity probably resides in the spinal nerves.

Behavioural experiments support the relevance of the mucoid stimulus for the rocklings and provide additional evidence that the ADF, not the nose, is the specific site of perception (Kotrschal *et al.*, 1989, 1991). Fish react to standard-test mucus dilutions (sources: *Lophius* sp., goosefish and *Opsanus* sp., frogfish) of 1 : 1000000 with a decrease in locomotory activity. Also, breathing ceases immediately at stimulation and is irregularly resumed shortly afterwards. Experiments to isolate the active component of fish mucus have not yet been performed.

The analysis of ADF sampling patterns supports the hypothesis that the ADF-SCCs are the sensors of a low-threshold mucus-detecting system (Kotrschal *et al.*, unpubl.). Adaptation of the ADF system occurs within 1.5 s. However, even at constant stimulus concentrations, rocklings may shift their adaptation–disadaptation equilibrium and thus their ADF sampling frequency. Each start from rest or change in frequency of the ADF results in a new response; for example when the ADF is moving at 14 Hz and already adapted, a new response can be recorded when the ADF speeds up to e.g. 16 Hz (Peters *et al.*, 1989, 1991). It is hypothesized that the high-frequency ADF motion increases the change of water and decreases boundary layers around the SCC apices, and serves a function analogous to vertebrate nose sniffing or crustacean antennulae flicking (Atema, 1987, 1988; Moore and Atema, 1988).

Hypotheses on SCC functions and biological roles

The rockling ADF is a superior model for investigating structure, central connections, function and biological roles of SCCs. Responses to heterospecific fish mucus (Kotrschal *et al.*, 1989; Peters *et al.*, 1987, 1989, 1991) suggest that the ADF-SCCs may be involved in predator avoidance.

Yet it remains uncertain whether the results obtained from the rockling ADF model apply to the majority of scattered, generalized SCC systems in the actinopterygian fishes (Figs 1 and 2); we do not even know whether the ADF results are applicable to the SCCs scattered over the rockling's body surface. The possibility remains that the SCCs is the rockling ADF are used in a specialized way; clearly, data from generalized SCC systems are needed.

Baatrup and Doving's (1985) electrophysiology of lamprey SCCs (oligovillous cells) supports the rockling results. Best responses were obtained with trout mucus, water in which a frozen trout was allowed to thaw and with sialic acid, whereas most amino acids elicited only minor responses (Baatrup, 1984 a,b).

In the sea robin, however, Silver and Finger (1984) recorded responses from spinal nerves innervating the free pectoral fin rays, to food-related stimuli and to amino acids. The claviform bodies of the epidermis of these fin rays contain SCCs (Whitear, 1971), but it remains uncertain whether Silver and Finger (1984) recorded from SCC units. Still, these results indicate the possibility that the use of SCCs may be flexible in fish, depending on innervation and selection pressures.

In the rocklings, sensing of dilute fish mucus by the ADF elicits arousal, indicated by a temporary cessation of breathing and a decrease in locomotory activity (Kotrschal *et al.*, 1989, unpubl.). Electrophysiological responses from the sensory nerve could only be picked up when the ADF was undulating (Peters *et al.*, 1989). Therefore, undulation of the fin can be seen as a means of sampling. ADF sampling intensifies, not only in response to specific stimulation, but with any arousal by sensory input (Kotrschal *et al.*, 1991). It seems that the active ADF allows rocklings to sample accurately while at rest. To achieve a comparable effect, the majority of fish with a generalized, scattered SCC distribution would have to utilize swimming speed. The ADF movement in the benthic rocklings thus efficiently decouples SCC sampling from locomotion and allows the resting fish to sample accurately.

Chemically aroused fish such as the fathead minnow (*Pimephales promelas*) indeed show increased swimming speed over short distances, resulting in dash swimming

(Lawrence and Smith, 1989); in alternation with dash swimming, fish may freeze. Dash swimming in aroused fish is commonly thought to increase the likelihood of escaping a predator. However, dashing or enhanced swimming speed may decrease the boundary layer around chemoreceptors at the body surface and thus, by analogy to the rockling ADF, improve their sensory performance.

SCCs were found to be particularly numerous at the body surface of cyprinids (Kotrschal, in press). Whether SCCs, in addition to the nose, are involved in detecting alarm substance (Frisch, 1938, 1941; Pfeiffer, 1977) is not known. Cyprinids have been tested in olfactometers to elucidate their differential behaviour towards conspecific components from intact and damaged skin (e.g. Berti *et al.*, 1989; Saglio and Blanc, 1989), but to my knowledge no attempts have been made to test behavioural responses to skin surface washes of heterospecifics and potential predators. The lamprey and rockling results suggest that it would be instructive to conduct such experiments.

Combining these SCC results with what is known about Schreckstoff (or alarm substance) perception (Frisch, 1938, 1941; Pfeiffer, 1977; Smith, 1982) leads to speculations about two lines of chemosensory-mediated predator avoidance in fish.

The first line may be mediated by allomones (chemical signals between species). Downstream of each fish, and thus also of potential predators, SCCs of other fish may detect the water-borne mucous stimuli; specific predator-avoidance reactions may be elicited even before visual clues become effective (Pitcher, 1986). Quantity of release, characteristics of the carrier current and characteristics of the receptor system determine the effective radius (Okubo, 1980).

If this first line of chemo-avoidance (e.g. elicited by downstream approach by the predator) and other means fail, a second line of pheromonic (intraspecific) chemocommunication becomes effective, at least in ostariophysan fishes: alarm substance from the club cells of handled individuals, which (Lawrence and Smith, 1989) triggers intense predator-avoidance behaviour (Frisch, 1938, 1941). The site of Schreckstoff perception is probably the olfactory epithelium, as may be generally the case with pheromones; for instance, extreme olfactory specificity for a pheromone was shown for goldfish (Sorensen *et al.*, 1990).

Whether or not this chemosensory scenario is realistic, the structural and functional data on SCCs justify an increase and re-definition of the number of chemosensory input channels in teleosts, as also suggested by Baatrup (1984b), who linked SCCs with a 'third chemical sense'.

To be recognized as a distinct chemosensory input channel, systems must qualify by a distinct morphology (peripheral receptor, innervation, central connections) and by distinct functions and biological roles. This definition excludes primary mechanisms at sensory-cell apical receptor membranes, which may be diverse in similar cell types (Kinnamon, 1988) and may change relatively rapidly in the course of molecular evolution.

Assuming that the terminal nerve (Demski and Schwanzel-Fukuda, 1987) is indeed chemosensory, that SCCs are distinct, and defining the 'common chemical sense' more rigidly (see below) as being associated with free spinal or trigeminal nerve endings, we can now distinguish five distinct chemosensory input channels in fish (Table 1). Three of these are mediated by primary sensory cells: conventional olfaction, the olfacto-retinalis or terminalis system, and trigeminal or spinal nerve endings or dorsal root ganglion cells (the common chemical sense). The two remaining, taste (via TBs) and the SCCs chemo-

Table 1. Summary of proposed sensory input channels in teleost fish, listing their morphological substrate (= sensory cell), cell type (primary or secondary), central connection (termination areas of sensory afferents in the central nervous system), functions (neuronal responses to stimuli) and biological roles (behavioural responses and ecological context). There is no direct evidence for a sensory function of the nervus terminalis system (Demski and Schwanzel-Fukuda, 1987).

Chemosensory input channel	Morphological substrate	Sensory cell type	Central connections	Functions	Biological roles
1. Olfactory system	Olfactory neurones	Primary	Olfactory bulb	Low-threshold, wide-spectrum discrimination	Food search, chemo-learning and social behaviour
2. Nervus terminalis system	Olfacto-retinalis neurones	Primary	Retina, hypothalamus	(?)	Reproduction (?)
3. Free nerve endings ('common chemical sense')	Trigeminal or spinal afferent neurones	Primary	Brain stem, spinal cord	High-threshold discrimination of aversive stimuli	Avoidance behaviour
4. Taste	Taste buds	Secondary	Brain stem viscerosensory lobe	Close-range (food) discrimination	Feeding
5. SCC chemosense	Solitary chemosensory cells	Secondary	Brain stem	Low-threshold mucus discrimination	(1) Predator or general avoidance; (2) Feeding (?)

sense, are mediated by secondary sensory cells.

The rockling findings shake a century-old dogma of skin chemosensation, as in the case of the ADF a non-feeding biological role is associated with the special viscerosensory (Herrick, 1899), facial, afferents, which seemed until now to be related to feeding-associated taste (and touch, Davenport and Caprio, 1982; Marui and Caprio, 1982). Thus part of the recurrent facial nerve fibres in rockling seem to mediate a behaviour which was previously associated with the general cutaneous nerve components and with the common chemical sense avoidance reactions. This shows that the special viscerosensory facial system may possess a wider spectrum of biological roles than just feeding.

Another exception to Herrick's (1899) association of sensory nerve components with biological roles is the sea robin's pectoral fin. There SCCs are innervated by general cutaneous nerve components (spinal) and are seemingly used in the search for food (see below). Also, in other fish that are known to have SCCs but lack a recurrent facial nerve, such as sticklebacks (Whitear, 1971), SCCs may be innervated from general cutaneous sources.

Are SCCs the morphological substrate for the 'common chemical sense'?

When Parker (1912) denervated TBs of the flank in *Ictalurus*, a catfish, he still found those skin areas to be chemosensitive. This 'common chemical sense' was hypothesized to reside in spinal free nerve endings. The higher threshold of the common chemical sense, as compared to the special visceral (facial, connected with TBs) components, seemed compatible with this hypothesis. Also, the behaviour elicited by stimulation of the common chemical sense was avoidance rather than food search (Bardach, 1967; Bardach *et al.*, 1967).

Whitear (1971) suggested that SCCs may bridge the tight junctions of fish epidermis (which may prevent stimulus access) and serve as the end-organs of this common chemical sense. However, the results from the rockling ADF have cast doubts on this interpretation. The connection of the ADF-SCCs with facial components, their low thresholds and their narrow specificity for fish mucus do not fit the original definition of the common chemical sense, but rather make SCCs, besides the TBs, a further sensory component of the special visceral sensory system, at least in the rocklings.

It is not known at present whether the majority of generalized, scattered SCC systems connect with general cutaneous components (trigeminal and spinal), as in the sea robin in rays, or with the special visceral component (facial), as in the rocklings. However, in a majority of teleosts, a recurrent facial nerve is present, which supplies the trunk TBs (Freihofer, 1963). Only in a few groups, among them sea robins, is this recurrent facial nerve seemingly lacking. Selective tracing with the carbocyanine dye DiI of facial or spinal nerves in the rockling pelvic fin indicates that there too, SCCs synapse with the facial, not with the spinal, nerves (Kotrschal, unpubl.).

The sea robin's free pectoral fin rays (Fig. 1) provide an example of SCCs synapsing with spinal nerves; Scharrer (1935) showed that the common chemical sense, which normally gives rise to avoidance reactions, is here used in foraging (Bardach *et al.*, 1967; Silver and Finger, 1984). Therefore, Bardach (1967) was reluctant to link the sea robin fin ray chemosensitivity with the common chemical sense. The question of including SCCs in the common chemical sense has become even more complicated when one compares the sea robin with the rockling results.

It seems today that it is largely a matter of definition, whether or not the common chemical sense is accepted as a valid chemosense. Olfaction and taste are unambiguously associated with their morphological substrates, receptors and central pathways (finger, 1988; Getchell and Getchell, 1987), as well as functions (Caprio, 1988). This is not so with the common chemical sense. There is ambiguity with respect to its end organs, free nerve endings or SCCs, its central connections, general cutaneous or special visceral components, and its biological roles, avoidance or food search.

Today the question of whether or not a common chemical sense exists and how it is to be defined seems only of limited heuristic value. As our knowledge on vertebrate skin chemosenses becomes more refined, the necessity of keeping a relatively empty and ambiguous term alive becomes questionable.

The term 'common chemical sense' may still be useful to distinguish olfaction and taste from trigeminal naso-pharyngeal chemoreception (Silver, 1987); however, it may take considerable ambiguity out of the scientific discussion to talk specifically about 'trigeminal chemoreception' in this case. Whenever SCCs are involved, the arbitrary term 'SCC chemosense' is suggested until more is known about central connections and functions of generalized SCC systems. Also, free nerve endings (Whitear, 1983) should be named according to their structure or the sensation they mediate. In agreement with other authors (Bardach and Atema, 1971; Buddenbrock, 1952; Frisch, 1926) I therefore suggest that the notoriously ambiguous term 'common chemical sense' be dropped, in favour of more specific, and structurally and functionally more meaningful, names, now increasingly available for vertebrate chemosenses. If used at all in the future, the term 'common chemical sense' should be strictly associated with free trigeminal or spinal nerve endings, to be congruent with Herrick's (1899) definition of the general cutaneous nerve component.

Phylogeny of SCCs or: why taste buds at all?

In gnathostome vertebrates, the fine structural similarity between SCCs and TB receptor cells (Whitear, 1965, 1971) justifies the hypothesis that in vertebrate evolution, either TBs evolved by aggregation of SCCs, or SCCs are dispersed TB cells, unless one assumes that both types of organization evolved simultaneously. The only indication for evolutionary polarity from the SCCs to TBs is that TBs are structurally, and probably functionally, more complex than SCCs and therefore emerged later in phylogeny. However, this hypothesis remains untestable by a comparative approach, as no surviving vertebrate species ae available that carry only TBs or only SCCs.

Lampreys are the 'lowest' vertebrates from which data are available. The following considerations are not intended to imply that lampreys are direct gnathostome ancestors; they merely represent a relatively well-known example of sub-gnathostome organization. TB-like organs seems to be present in hagfish (Georgieva *et al.* 1979), and probably SCC-like cells, too (Schreiner, 1918). Lampreys possess both TB-like terminal buds (Baatrup, 1983 a,b, 1984 a,b) and SCC-like oligovillous cells (Whitear and Lane, 1983). Yet there are striking differences between terminal buds and oligovillous cells in how receptor cells contact afferent nerve fibres. Lamprey oligovillous cells show apical microvilli and are relatively close in fine structure to actinopterygian SCCs, whereas terminal bud receptors are ciliated, which is not the case in any other vertebrate taste bud.

These lamprey data allow for a spectrum of hypotheses concerning the phylogenetic relationships between SCCs and TBs, all of which are as equally likely as they remain untestable:

1. Agnathan terminal buds with their ciliated receptor cells are TB analogues, which were replaced in the gnathostomes by TBs assembled from the microvillous SCCs.
2. Receptor cells in agnathan terminal buds eventually de-ciliated and developed into the typical microvillous TB receptor cells (Baatrup, 1983 a,b, 1984b). The vertebrate olfactory epithelium provides an example that such a change in the apical receptive structures may occur. In this case the close fine structural similarity between TB receptor cells and SCCs in the gnathostomes is due to similar functions rather than to origin from a common cell line.

The association of similar receptor cells with two different forms of organization, SCCs and TBs, evokes the question, why do TBs exist at all? What functions could not be equally well performed by a dispersed system? The following considerations on functional differences between TBs and SCCs also aim at identifying selection pressures which may have led to their evolution and maintenance in parallel, for at least 400 million years.

Intra-TB structural, particularly synaptic organization (Jakubowski and Whitear, 1990; Kinnamon, 1987) suggests that TBs can be compared with microprocessors (Roper, 1989). Two functional principles of TBs particularly come to mind which could not possibly be performed by a dispersed system: peripheral coding, and exact spatio-temporal co-localization of tactile and chemical stimuli.

A number of recent studies indicated that different sensory units of peripheral ensembles of chemosensory cells may respond differently to the same stimulus (e.g. Caprio, 1988; Casterline *et al.*, 1990; Dionne, 1990; Kohbara *et al.*, 1990; Michel and Ache, 1990; Weinstein *et al.*, 1990). This diversity of peripheral units allows for complex coding and thus for recognition of a wide variety of complex mixtures. Elements of integration in taste buds may be: the convergence of more than one receptor cell onto one afferent nerve fibre and a modulatory role of the latter (Finger *et al.*, 1990); the basal cells, if present (e.g. absent in some gadids, Jakubowski and Whitear, 1986, 1990) may play a modulatory or even interneurone-like (Delay and Roper, 1988; Kinnamon, 1987; Roper, 1989); some of the receptor cells within a taste bud may also be electrically coupled (Yang and Roper, 1987).

Tactile stimulation, if properly integrated, adds high spatio-temporal fidelity to chemosensation. All recordings from afferent facial components, except for the fibres coming from the rockling ADF, revealed clear tactile responses (Davenport and Caprio, 1982; Marui and Caprio, 1982; Peters *et al.*, 1991). Whether these originate from intra- or perigemmal fibres in unknown. It can be assumed that, comparable to the vagal lobe (Kanwal and Caprio, 1988), also in the facial lobe, taste and tactile maps overlap closely. This provides the fish with an integration of the exact spatio-temporal features of a tactile with a chemo-stimulus, the spatio-temporal locability of which is inherently much less precise than that of a tactile stimulus. Thus, one of the great benefits of TBs as compared with a scattered system appears to be the high-fidelity integration of three different stimulus-vectors; time, space and chemical quality.

If this argument applies for TBs, the reverse should apply for a dispersed, scattered SCC system. One can predict that comparatively little peripheral coding is possible in SCCs (if the SCC population is homogeneous). Thus SCCs should respond to only a limited number of stimuli as compared with TBs. A dispersed system thus should be most useful to monitor environmental levels (and changes thereof) of a restricted number of stimuli, bearing no necessity for integration with tactile information. As opposed to TBs, the system is not designed for close-range localization. Also, the even distribution of sensory cells of dispersed SCC systems, compared with TBs in the same animal, suggests bulk-water sampling. These predictions are indeed supported by the available SCC data from rocklings (see above).

All we know at present about SCCs is merely a glimpse. An entire, basic vertebrate chemosense is virtually unexplored, offering a vast and rewarding field for further research. Now, data allow only for an educated guess that the biological role of SCC systems may rather be predator avoidance than prey detection. In-depth knowledge of the SCC chemosense seems of crucial importance for understanding the biology, the behaviour and the evolution of teleost fishes and vertebrates in general.

Summary

Secondary solitary chemosensory cells (SCCs) occur scattered within the epidermis of lampreys, teleosts and ranid tadpoles. Counts in representative telost species revealed that SCC's outnumber chemosensory cells organized in taste buds. Therefore, SCCs may be considered the structural substrate of a basic and probably important vertebrate chemosense. However, detailed information on structure, innervation and function is only available from specialized fins in a few teleost species, where SCCs are sufficiently concentrated. The foremost research model has been the anterior dorsal fin (ADF) in rocklings, which contains millions of SCCs but no other specialized chemosensory elements. It has been shown that these ADF-SCCs are innervated from the recurrent facial nerve. Electrophysiological recordings revealed that there is virtually no overlap in stimulus spectrum between the ADF-SCCs and pelvic fin taste buds; SCC responses could only be triggered by dilutions of heterospecific fish body mucus. Results of behavioural experiments indicate that fish mucus is indeed a relevant stimulus. Therefore it is hypothesized that the biological role of the ADF-SCCs is predator avoidance rather than search for food. Whether these findings are valid for rockings only, or can be generalized for the scattered SCC systems in more than 20000 species of fish and in some amphibians, remains an open question. Further investigations on the function and biological roles of the SCC chemosense will be crucially important to improve our understanding of sensory perception and its evolution in aquatic vertebrates.

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