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VOLTAGE-ACTIVATED IONIC CURRENTS IN MYOEPITHELIAL CELLS ISOLATED FROM THE SEA ANEMONE *CALLIACTIS TRICOLOR*

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Summary

Myoepithelial cells were isolated from the apical ends of mesenteries of the sea anemone *Calliactis tricolor* and examined using the whole-cell configuration of the patch-clamp technique. The isolation procedure produced cell fragments that were contractile and produced action potentials when depolarized. These action potentials are formed by a complex array of ionic currents consisting of at least one, and possibly two, inward calcium currents and four outward potassium currents. The ionic selectivity of the calcium currents was $Ca^{2+}>Sr^{2+}>Ba^{2+}$. Outward currents consisted of a calcium-dependent outward current and three voltage-activated currents, including a 4-aminopyridine-sensitive current, a transient outward current and a steady-state current.

Introduction

Cnidarians are the simplest extant organisms to possess a nervous system and as such, have been the focus of much research directed at understanding the properties of the 'first' nervous systems (for reviews, see Satterlie and Spencer, 1987; Anderson and Schwab, 1982; Anderson, 1989; Anderson and Spencer, 1989). In recent years, following the development of preparations of giant or otherwise accessible neurones, the focus of much of this work has become increasingly cellular and has provided important information about the basic properties of these nervous systems.

The only cnidarian class where cellular electrophysiology studies are lacking is the Anthozoa. This stems largely from the complexity of the tissue, the prohibitively small size and diffuse distribution of neurones in these organisms, and the fact that their tissues are frequently spontaneously contractile. These factors impose severe restrictions on the techniques that can be applied to these animals and, as a result, on the quality of information that can be obtained from them.

Key words: sea anemone, Anthozoa, voltage-clamp, calcium currents, potassium currents, myoepithelial cells, *Calliactis tricolor*.

Here we report the results of voltage-clamp experiments with myoepithelial cells isolated from a sea anemone. The data indicate that these cells are electrically excitable, and produce fast, overshooting action potentials that are carried by one, possibly two, calcium (Ca^{2+}) and four potassium (K^+) currents. In many respects the properties of these currents are similar to equivalent currents in other organisms, but they also display some noteworthy features, such as an abnormal hierarchy of permeability with respect to the inward currents.

Materials and methods

Specimens of the anemone *Calliactis tricolor* (Le Sueur) were collected locally and maintained in running seawater aquaria, where they survived for many months on a mixed diet of marine organisms.

Prior to dissection, animals were relaxed for about 1 h in a 1:1 mixture of sea water and isotonic $MgCl_2$ ($0.34\,mol\,l^{-1}$). The upper quarter of the animal was cut off and opened up with a single radial cut from the margin to the mouth. The resulting strip of tissue was then pinned out and the pharynx and oral disk removed, the latter by cutting the mesenteries at their points of insertion on the underside of the oral disk, and then cutting around the margin of the disk. This step revealed the apical end of the mesenteries. At their marginal edges, where they meet the tentacles, the incomplete mesenteries have an obvious red/purple coloration. Pieces of this pigmented tissue were then dissected free and transferred to sea water. The myoepithelial cells ultimately obtained from this tissue have the advantage of being from an area that contains no gonads and a minimum of ciliated cells, with the result that the suspensions of isolated cells were cleaner and essentially devoid of motile (ciliated) cells.

The tissues were then digested in papain [Sigma type IV, at $3.75\,mg\,ml^{-1}$ in artificial sea water (ASW, see below), activated with $0.5\,mg\,ml^{-1}$ dithiothreitol (Sigma) at pH 8.0] for 1 h, then transferred to fresh ASW and maintained at 10°C until needed. To isolate cells, pieces of enzymatically treated tissue were triturated through a fine glass pipette or a 22 gauge needle. The resulting cell suspension was then transferred to the lid of a 35 mm Falconware Petri dish, and cells were allowed to settle and adhere. In experiments involving media other than normal ASW, cells were triturated in the medium of choice.

Whole-cell voltage-clamp experiments were carried out in the manner described previously (Anderson, 1987). Briefly, cells were voltage-clamped in the whole-cell configuration using a Dagan 8900 patch clamp amplifier. Pipettes were pulled from borosilicate glass and filled with one of the solutions given below. Seals were obtained by gently pushing the pipette against the cell surface, any offset currents having first been neutralized, and applying gentle suction. With these cells, seal formation was greatly facilitated by imposing a negative potential (up to −70 mV) on the pipette. Pipette capacitance was neutralized and additional suction applied to achieve the intracellular configuration. At this point, series resistance compensation was added. Voltage protocols were applied and data acquisition and

manipulation carried out using an IBM AT computer equipped with pClamp software (Axon Instruments). Capacitative and leakage currents were subtracted on-line, using software routines.

Solutions

Artificial sea water (ASW) had the following composition (mmol l^{-1}): NaCl 395; KCl 10; $CaCl_2$ 10; $MgCl_2$ 50; Hepes buffer 10; pH 8.0. Barium- (Ba^{2+}) and strontium- (Sr^{2+}) containing ASWs were made by direct substitution of Ca^{2+}. Na^+-free ASW was prepared using Tris chloride or choline chloride, Ca^{2+}-free ASW by substitution with Mg^{2+}. Patch pipettes were filled with either a normal intracellular solution containing (mmol l^{-1}): KCl 140; $CaCl_2$ 1; EGTA 11; Hepes buffer 10, or a caesium/tetraethylammonium (Cs^+/TEA^+) solution consisting of (mmol l^{-1}) CsCl 70; TEACl 70; $CaCl_2$ 1; EGTA 11; Hepes buffer 10. The pH of both solutions was adjusted to 7.0 with KOH or CsOH. All experiments were carried out at room temperature (20–22 °C).

In experiments involving changes in external medium, a suspension of cells was placed near the middle of a narrow, 1 cm long, plastic, U-shaped insert which was glued to the centre of the preparation dish. The volume of this insert was 200–250 μl. Prior to recordings in the first solution, the bulk of the medium outside the insert was removed, leaving just enough to achieve electrical continuity between the insert and the bath ground. Fluid was retained in the insert by the narrow neck at the open end. To change bathing solutions, 1 ml of the new solution was added to the closed end of the insert *via* a fine, plastic pipette. Since the volume of solution added was 4–5 times that of the insert, the medium within the insert was changed 4–5 times, with the new solution inevitably flowing over the cells and out of the insert at the open end. Solution replacement typically took 15–30 s. If necessary, the first solution was then reapplied in the same manner.

Results

Appearance of cells

Cells isolated from the pigmented region of the incomplete mesenteries of *C. tricolor* had two general morphologies. The majority of freshly isolated cells had the very elongate appearance one might expect of muscle cells, and were contractile. In addition to the elongate fragments, there were always many 20–30 μm roughly spherical cells, which were characterized by the presence of numerous red/purple pigment spots. No obvious differences were noted in the electrophysiology of either cell type.

Basic electrophysiological properties

Electrophysiological examination of cells bathed in ASW, using the high-K^+, low-Ca^{2+} patch solution proved difficult because the cells invariably contracted after breakthrough, often to the extent that they detached from the pipette. Nevertheless, sufficient recordings were obtained to provide information on the basic electrical properties of these cells.

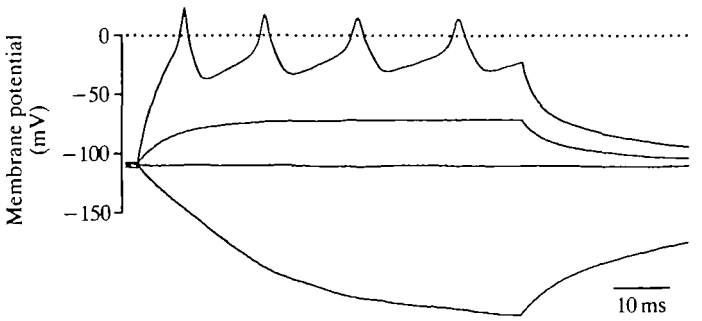

Fig. 1. Current-clamp recording from a myoepithelial cell from *Calliactis tricolor*. This cell was hyperpolarized to a membrane potential of −110 mV and responded to injection of depolarizing and hyperpolarizing current pulses in the manner shown.

Isolated cells examined with patch electrodes filled with the normal intracellular solution had resting potentials between −60 and −90 mV. When depolarized by current injection, these cells spiked repetitively, at frequencies of up to 50 Hz (Fig. 1). The action potentials themselves were relatively fast, overshooting events. Maximum rate of depolarization was 42.5 $V s^{-1}$ and they repolarized at a rate of up to 16.6 $V s^{-1}$ with a time constant of 1.47 ms.

Total membrane currents

A typical family of total membrane currents in these cells consisted of a small, relatively slow, transient inward current that activated at around −20 mV and a large, complex outward current that activated at around −15 mV (Fig. 2). This same family of currents was seen in all cells examined, regardless of morphology. However, in early experiments, inward currents were either completely absent from all cells examined, or disappeared very rapidly after cell isolation, regardless of the treatment given to the cells. This was later traced to an effect of prolonged Mg^{2+} anaesthesia and prompted us to keep this to a minimum. The cell dissociation protocol described in the Materials and methods section is that which evolved to minimize Mg^{2+} exposure.

Inward currents

With the exception of a very brief, small outward deflection at the onset of the voltage step (see below), all outward current was readily blocked by replacing the 140 mmol l^{-1} K^+ in the patch pipette with a combination of 70 mmol l^{-1} Cs^+ and 70 mmol l^{-1} TEA^+, allowing examination of the inward currents in isolation. Cells did not contract with this patch solution. Total inward current was a transient current that activated between −20 and −25 mV, reached maximum amplitude close to 0 mV and reversed around +50 mV (Fig. 3A,B). Mean time to peak of the maximum inward current was 4.0±0.3 ms (S.E.M.; N=10) and it decayed with a time constant of 18.8±3.3 ms (N=10). Tail current analysis suggests that there may be two components to the inward current. For voltage steps to potentials of less

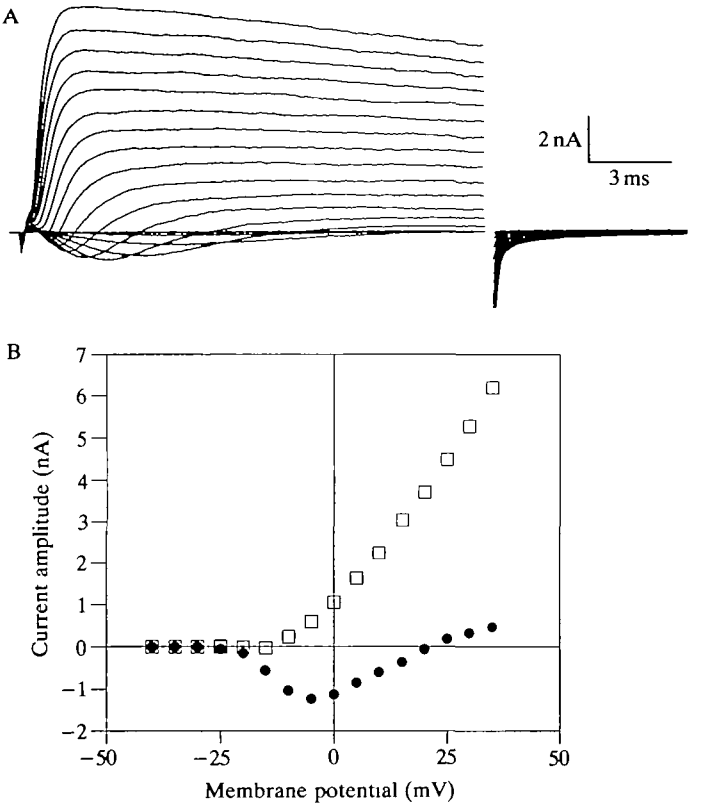

Fig. 2. Voltage-clamp recording of the total membrane currents in an isolated myoepithelial cell. (A) Total membrane currents generated by a series of depolarizing voltage steps. The first step was to −40 mV with subsequent steps increasing by 5 mV. Holding potential −100 mV. (B) Current/voltage relationships of the peak outward (□) and inward (●) currents recorded in A.

than 0 mV, there was a single fast tail current, which had a time constant of 0.2±0.01 ms (N=21) (Fig. 3C). At potentials more positive than 0 mV, a second tail current, with a time constant of 2.7±0.3 ms (N=20), appeared. The waveform of the total inward current did not change in any obvious manner coincident with the appearance of the second tail current.

Total inward current diminished with time, presumably reflecting washout or rundown. The time course and degree of washout of the inward current varied considerably from cell to cell but the typical effect was to reduce the overall amplitude of the inward current and to transform it from a slowly decaying transient current (Fig. 3A,C) to a more steady-state current. There was never any obvious change in the amplitude or appearance of the inward tail currents coincident with washout.

Inward current in these cells inactivated in a voltage-dependent manner. Twin

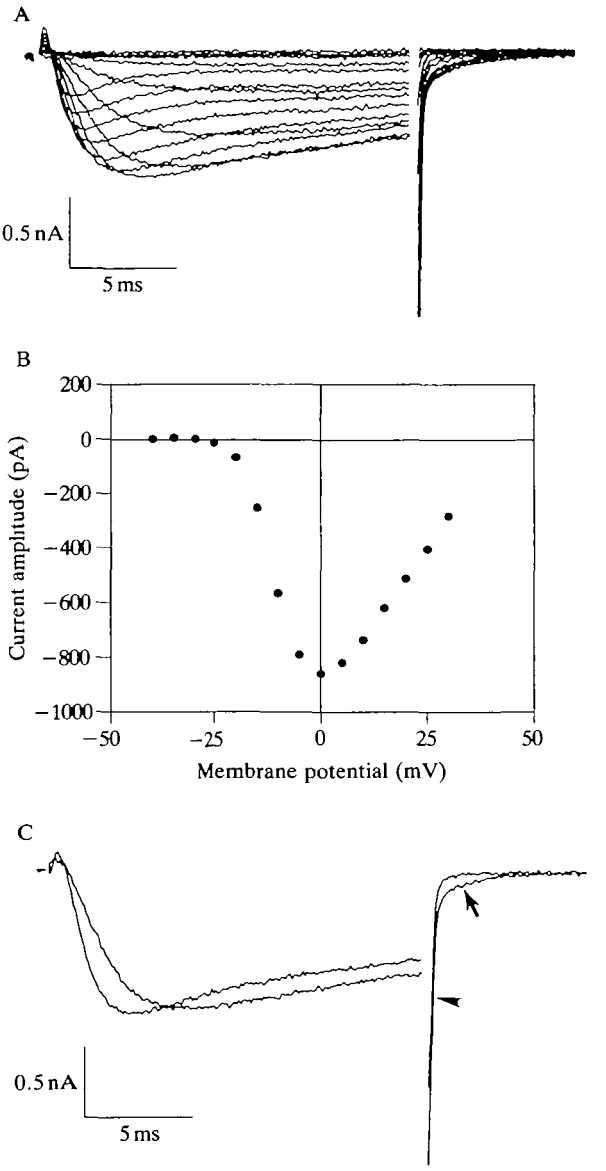

Fig. 3. Inward currents in isolated myoepithelial cells. (A) A family of inward currents evoked by depolarizing steps from a holding potential of −100 mV to −40 mV, with subsequent steps increasing by 5 mV. Patch pipette contained Cs^+/TEA^+ to block outward currents. (B) Current/voltage relationship of the currents recorded in A. (C) Currents recorded following voltage steps to −5 mV and +5 mV from a holding potential of −100 mV. The first current has a tail current with a single, fast time constant (arrowhead), while the tail current associated with the second current has both fast and slow (arrow) components.

pulse experiments designed to measure the coefficient of steady-state inactivation ($H\infty$), using prepulses of 100, 500 and 1000 ms duration, showed that the mean threshold for inactivation was -41.3 ± 4.1 mV ($N=8$), and the potential at which the current was half-inactivated was -21.7 ± 1.3 mV ($N=8$). That these numbers were the same irrespective of prepulse duration suggests that there is only a single component of inactivation in these cells. Recovery from inactivation had a time constant of 15 s (data not shown).

Inward current in these cells is carried by Ca^{2+}. No inward current was recorded in Ca^{2+}-free ASW containing 10 mmol l^{-1} EGTA, and both the voltage-dependency and waveform of the inward current were unaffected by removal of all extracellular Na^+ (Tris or choline substitution), or the presence of tetrodotoxin (TTX) (1 μmol l^{-1}). The ion selectivity of the Ca^{2+} channels was determined by replacing the Ca^{2+} in the bath with Sr^{2+} (Fig. 4A) or Ba^{2+} (Fig. 4B). Inward currents in each case were smaller. Replacement of Sr^{2+} with Ba^{2+} also resulted in a reduction of inward current (Fig. 4C). The ion selectivity was thus shown to be $Ca^{2+}>Sr^{2+}>Ba^{2+}$. Inward current in these cells was reversibly blocked by 5 mmol l^{-1} cadmium (Cd^{2+}) (Fig. 4D), 5 mmol l^{-1} cobalt (Co^{2+}) (Fig. 4E) and 50 μmol l^{-1} verapamil (Fig. 4F). Nifedipine (10^{-4} mol l^{-1}) was ineffective.

The only outward current not blocked by intracellular Cs^+/TEA^+ was a small transient current recorded immediately after the voltage step (Fig. 3A). This current first appeared around -20 mV and became progressively larger at more depolarized potentials. Although it was selectively enhanced when Ba^{2+} was the charge carrier, as opposed to either Ca^{2+} (Fig. 4B) or Sr^{2+} (Fig. 4C), it could not be abolished by any ionic manipulations.

Outward currents

To examine outward currents in isolation, all inward current was abolished by recording in Ca^{2+}-free ASW. Under these conditions, total outward current was a slow, transient current. Pharmacological and ionic manipulations revealed at least four distinct components to the total outward current in these cells.

Subtraction of currents recorded from the same cell in the presence and absence of extracellular 4-aminopyridine (4-AP) revealed a fast outward transient current (Fig. 5A). This current activated close to 0 mV (Fig. 5B). Its mean time to peak was 1.1 ± 0.01 ms ($N=7$) and it decayed with a time constant of 1.2 ± 0.2 ms ($N=7$). Twin pulse experiments, using 100 and 500 ms prepulses to various amplitudes, before and after addition of 4-AP, revealed that the current was unaffected by prepulses to -50 mV or more negative values, but was rapidly inactivated by more positive steps. The potential for half-inactivation was close to -20 mV.

A Ca^{2+}-dependent K^+ current was found in a similar series of experiments in which currents were recorded in the presence and absence of extracellular Ca^{2+} or in the presence and absence of 5 mmol l^{-1} Cd^{2+} (Fig. 6A–C). Subtraction of these records (Fig. 6D) revealed a complex current consisting of an early, inward-going current with a delayed, outward-going component. The inward current is clearly the normal inward Ca^{2+} current in these cells, but the observation that there is also

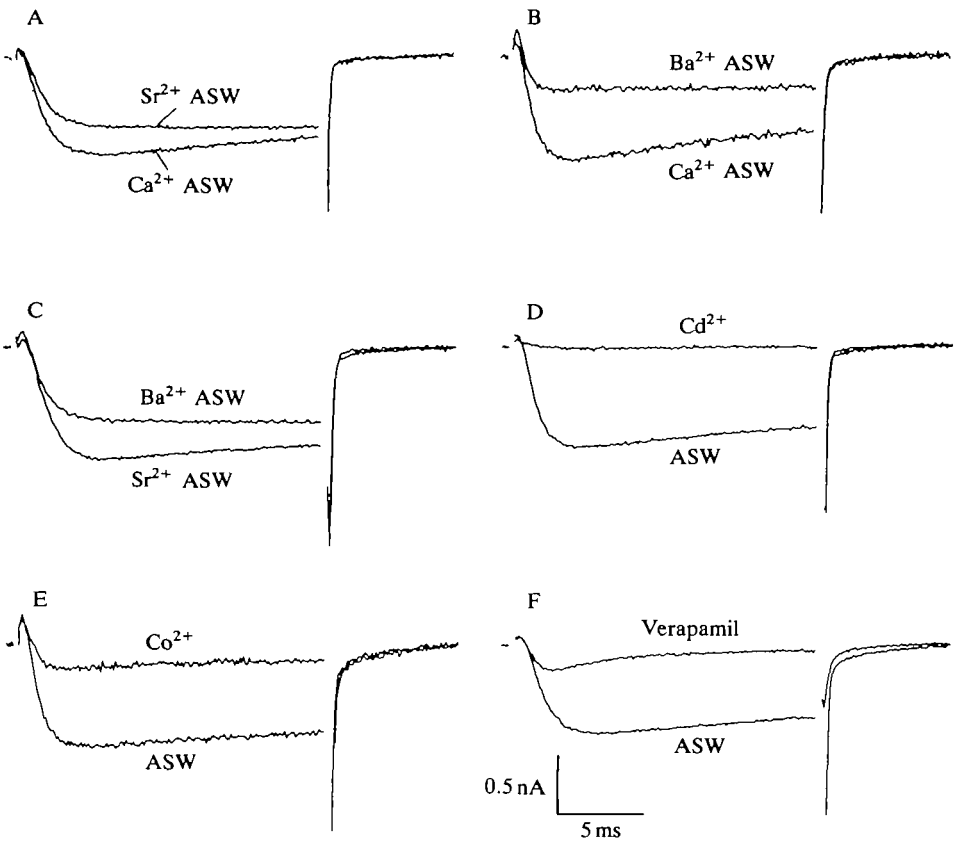

Fig. 4. Inward current selectivity and pharmacology. (A) Inward currents recorded from the same cell in response to the same voltage step (holding potential −100 mV, step potential +5 mV) in Ca^{2+}- and Sr^{2+}-containing artificial sea waters (ASWs). (B) The same, from another cell, in response to a voltage step to 0 mV, in Ca^{2+} and Ba^{2+} ASWs. (C) Inward currents recorded from a different cell bathed in Sr^{2+} and Ba^{2+} ASWs, in response to a voltage step to 0 mV. From this series of experiments, the ionic selectivity of this current was shown to be $Ca^{2+}>Sr^{2+}>Ba^{2+}$. (D) Inward currents recorded from the same cell in the presence and absence of 5 mmol l^{-1} Cd^{2+}. (E) Effect of 5 mmol l^{-1} Co^{2+} on inward current recorded in response to a voltage step from −100 mV to +5 mV. (F) The effect of 50 μmol l^{-1} verapamil on currents evoked by the same voltage paradigm, in another cell. The actions of verapamil, Cd^{2+} and Co^{2+} were all reversible.

an outward-going component indicates that there is an outward current that is also Ca^{2+}-dependent since it disappears in the absence of extracellular Ca^{2+} or when the inward Ca^{2+} current is blocked by Cd^{2+}. This current activated at around −10 mV and decayed slowly. The exact activation voltage of the Ca^{2+}-dependent current was difficult to ascertain owing to the presence of the contaminating inward current. Subtractions of the sets of traces underestimate the actual amount

of outward current for the same reason (Fig. 6D). This current was susceptible to internal Cs^+/TEA^+.

In Ca^{2+}-free ASW containing 5 mmol l^{-1} 4-AP, total outward current consisted of a slowly decaying transient current that activated at −20 mV. Total outward current reached peak amplitude in 3.2±0.3 ms (N=7) and decayed with a time

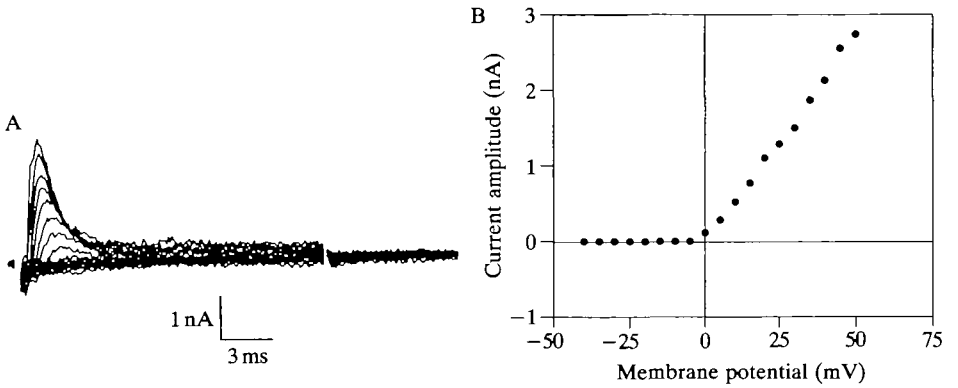

Fig. 5. (A) A fast, transient, A-type current revealed by subtracting families of currents recorded from the same cell in the presence and absence of 5 mmol l^{-1} 4-aminopyridine (4-AP). Both solutions were Ca^{2+}-free. Holding potential −100 mV, first voltage step to −40 mV, step potential +5 mV. (B) Current/voltage relationship of the currents presented in A.

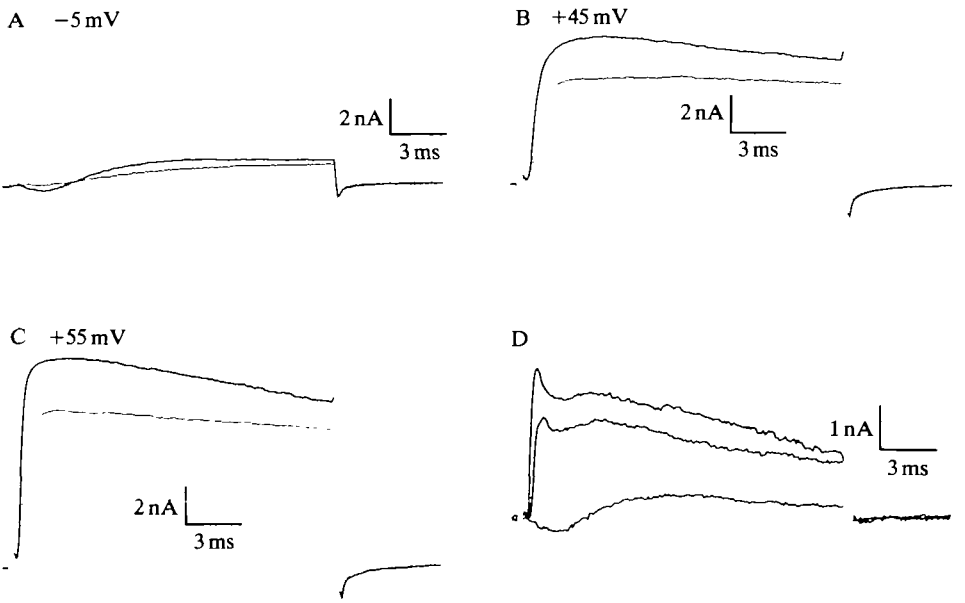

Fig. 6. (A–C) Outward currents recorded from the same cells before (solid lines) and after (dotted lines) the addition of 5 mmol l^{-1} Cd^{2+}, following voltage steps to −5 mV (A), +45 mV (B) and +55 mV (C). (D) The Cd^{2+}-sensitive inward and outward currents revealed by subtraction of the currents shown in A–C.

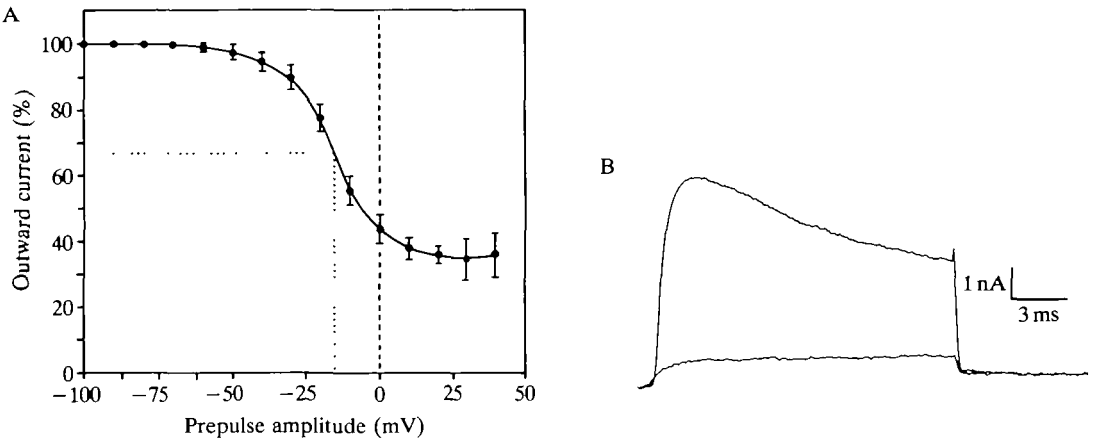

Fig. 7. (A) $H\infty$ plot of the outward currents recorded in Ca^{2+}-free ASW containing 4-AP. This graph is a plot of peak outward current generated by a voltage step to +40 mV following prepulses to the values shown on the abscissa. Current amplitude is expressed as a percentage of that recorded in the absence of any prepulses and each point represents the mean±S.E.M of six cells. The dotted line marks the potential for half-inactivation. (B) Outward currents recorded from one cell bathed in Ca^{2+}-free ASW containing 5 mmol l^{-1} 4-AP, in response to voltage steps to +40 mV from holding potentials of −70 mV and 0 mV. This protocol permitted separation of the transient component of the outward current from the steady-state component.

constant of 20.3±2.1 ms (N=13). This complex outward current could be dissected into a rapidly activating, slowly inactivating transient current and a steady-state current by selectively inactivating the transient component using depolarizing prepulses (Fig. 7). The mean threshold for inactivation of the transient current, calculated from $H\infty$ plots for each of eight cells, was −48.0±2.4 mV (N=8) and the voltage dependency of inactivation was shallower than those for all other currents in these cells, with mean inactivation occurring at −10.4±2.8 mV (N=8) (Fig. 7A). The current remaining after complete inactivation of the transient current (Fig. 7B) was indeed steady-state, showing essentially no decay over a period of 500 ms. Both of these currents were carried by K^+, as they could be abolished by internal Cs^+/TEA^+. Furthermore, tail currents recorded at the end of 1.5 ms and 18 ms voltage steps, when the transient and steady-state currents, respectively, were maximally active, reversed close to the predicted K^+ equilibrium potential and were dependent on the extracellular potassium concentration.

Discussion

Our understanding of the electrical properties of anthozoans is based almost entirely on extracellular recordings. Such recordings provide evidence for multiple conduction systems, specifically the through conducting nerve net (TCNN) and two slow systems, the SS1 and SS2 (McFarlane, 1982; McFarlane *et al.* 1989). However, we know essentially nothing about the cellular properties of the

excitable cells that constitute these conduction systems. Indeed, the possibility that the two slow systems might be epithelial conduction systems was ruled out only recently (McFarlane *et al.* 1989). The lack of cellular information stems from the various technical problems outlined above. Here we provide the first detailed description of the variety and properties of ionic currents in these animals.

All recordings presented here were obtained from a single cell type, fragments of myoepithelial cells found at the apical end of mesenteries in *Calliactis tricolor*. These cells were selected for technical reasons, and provided two distinct classes of fragment; elongate contractile fragments, which are presumably the contractile tails of the myoepithelial cells, and spherical pigmented structures that may be their cell bodies. The latter structures were also contractile. It should be stressed, however, that during the course of this and other studies we have recorded from a great many cells, predominantly myoepithelial cells, but also cnidocytes (McKay and Anderson, 1988), all of which came from a variety of tissues, in a variety of sea anemone species. In all cases but one, the recordings have been subjectively identical to those presented here. The only exception (P. A. V. Anderson, unpublished observations) is a brief recording from a putative neurone, tentatively categorized as such by its shape and the fact that it was phase-dark as opposed to phase-bright, as is the case for muscle cell fragments. The record from this neurone differed from those presented here in that the inward component of the total membrane currents was notably faster than the inward currents in muscle cells.

An important conclusion to be made from these data is that myoepithelial cells in sea anemones are electrically excitable. When depolarized, they produce action potentials which, judging from the results of the voltage-clamp studies, are Ca^{2+}-dependent. The action potentials we recorded were very attenuated in comparison with those recorded from, for instance, jellyfish neurones, using the same methods (Anderson, 1985), possibly because the recording configuration may have been compromised by the contraction that inevitably accompanied breakthrough into the intracellular configuration. Nevertheless, the observation that spiking occurs in both the presumed cell body and the contractile tail suggests that the action potential provides the Ca^{2+} necessary for contraction. Curiously, contractions produced in muscle cells isolated from the sphincter of *Calliactis parasitica* by applications of endogenous neuropeptides (McFarlane *et al.* 1991) occur in the complete absence of any electrical event (P. A. V. Anderson and C. J. P. Grimmelikhuijzen, unpublished results), even though the cells possess the same array of voltage-activated currents as those reported here. The absence of electrical activity preceding contraction suggests that the Ca^{2+} required for contraction can be supplied by other, presumably intracellular, sources. This, in turn, raises the question of the function of the action potential in these cells.

These muscle cells possess a variety of voltage-activated ionic currents. Inward current in the cells is carried exclusively by Ca^{2+}, but it is not clear whether there are one or two populations of inward current channels. The evidence for two populations of inward current channels comes from analysis of the inward tail

currents (Fig. 3C), specifically from the presence of two distinct components of the inward current tails. However, the onset of the second inward tail current was never associated with any obvious change in inward current itself, suggesting that, if there is indeed a second population of inward current channels, the current gated by those channels is qualitatively similar to that gated by the channels with the fast tail current. The possibility that one component of the inward tail current is associated with the brief transient outward current that is not blocked by intracellular Cs^+/TEA^+ can be ruled out by the observation that this current was present throughout the range of potentials over which inward current was active. It did not change in any way coincident with the appearance of the second component of tail current. The identity of this fast outward-going transient is discussed in more detail below.

The selective loss of the transient nature of the inward current by rundown or washout may be interpreted as further evidence for two inward currents, with those channels responsible for the transient component of inward current being the more susceptible to washout. However, the loss of the transient component was never associated with any detectable change in time course or in the relative amplitudes of the two tail currents, as would be expected if one population of channels had been selectively lost.

Finally, it was not possible to distinguish between the two populations of inward current channels pharmacologically. Although there may appear to be differences in the appearance of currents carried by different charge carriers (the Ca^{2+} current in Fig. 4A, for instance, has a more prominent transient peak than the Sr^{2+} current in the same cell), these effects were not reproducible.

The ionic selectivity of the inward current in these cells, $Ca^{2+} > Sr^{2+} > Ba^{2+}$, is notable. In vertebrates, Ba^{2+} is typically as good a charge carrier as Ca^{2+}, if not better (Bean, 1989). The same is true for Ca^{2+} currents in molluscan neurones (Hagiwara and Byerly, 1981; Alkon *et al.* 1984; Kostyuk *et al.* 1985). In the protozoan *Stylonychia mytilus syngen I*, Ba^{2+}, Ca^{2+} and Sr^{2+} are equally effective (de Peyer and Dietmer, 1980). The ionic selectivity of the Ca^{2+} channel in sea anemone muscle cells is clearly different from that of the majority of other Ca^{2+} currents, but at this stage it is difficult to identify any particular phylogenetic or other lineages. The selectivity of Ca^{2+} currents in the hydromedusa *Polyorchis pennicillatus* is apparently the same as that reported here (J. Przysiezniak and A. N. Spencer, personal communication), indicating that it may be a common feature of Ca^{2+} currents in cnidarians.

These cells possess at least four outward currents. The waveform of the 4-AP-sensitive current is reminiscent of that of A-currents seen elsewhere in the animal kingdom (Aldrich *et al.* 1979) and it is quite reasonable to describe it as such. This A-current is a very minor component of outward current in these cells, but it is remarkable for its speed of activation and inactivation. In that sense, it closely resembles the A-current recorded from cnidocytes from the hydroid *Cladonema* sp. (Anderson and McKay, 1987). The function of the current in these cells is unknown, particularly in view of its relatively small size.

The cells also possess a Ca^{2+}-dependent outward current, which was not analyzed in any detail in this study. The major outward currents are the transient and steady-state voltage-activated currents (Fig. 7), which, judging by their sensitivity to conventional K^+ channel blockers and their dependency on extracellular K^+, are K^+ currents.

The final outward current revealed by this study was the very brief, transient outward-going current evident at the onset of voltage steps (Figs 3A, 4). Such currents are normally classified as gating currents, but this classification is inconsistent with the observation that the amplitude of this current changed with different charge carriers (Fig. 3B,C). Ionic manipulations failed to block this current, suggesting that, if it is indeed a distinct ionic current, it is very non-specific.

In conclusion, myoepithelial cells from sea anemones possess a complex array of ionic currents that presumably underlie the action potential in these cells. These currents are essentially the same as those in higher organisms, with a few notable exceptions. First, the Ca^{2+} currents have an unusual ionic selectivity. Second, the A-current is remarkably fast and, finally, as is the case with ionic currents in other cnidarians (Anderson, 1987), the voltage dependencies of these currents are shifted in the positive direction, as compared with those in excitable cells in other, higher organisms.

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