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Excitatory connections of nonspiking interneurones in the terminal abdominal ganglion of the crayfish

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Abstract The output effects of the nonspiking interneurones in the crayfish terminal abdominal ganglion upon the uropod motor neurones were characterized using simultaneous intracellular recordings. Inhibitory interactions from nonspiking interneurones to the uropod motor neurones were one-way and chemically mediated. The depolarization of the motor neurones with current injection increased the amplitude of the nonspiking interneurone-mediated hyperpolarization, while hyperpolarization of the motor neurone decreased it. By contrast, excitatory interactions from the nonspiking interneurones to the motor neurones were not mediated via chemical synaptic transmissions. These excitatory connections with the slow motor neurones were one-way while connections with fast motor neurones were bidirectional. Nonspiking interneurone-mediated membrane depolarization of the motor neurones was not affected by the passage of hyperpolarizing current. Each motor neurone spike elicited a time-locked EPSP in the nonspiking interneurones with very short delay (0.2 ms) that suggested electrical coupling between nonspiking interneurones and motor neurones. Nonspiking interneurones directly control the organization of slow motor neurone activity, while they appear to regulate the background activity of the fast motor neurones. A single nonspiking interneurone is possible to inhibit some inter and/or motor neurones via direct chemical synapses and simultaneously excite other neurones via electrical synapses.

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Abbreviations

AL	Antero-lateral
cl	Closer
EPSP	Excitatory postsynaptic potential
mn	Motor neurone
ns int	Nonspiking interneurone
op	Opener
PL	Postero-lateral
r1	Nerve root 1
r2	Nerve root 2
r3	Nerve root 3
red mn	Reductor motor neurone

Introduction

Excitatory and inhibitory synaptic interactions are essential to process and integrate neural information. In many sensory systems of vertebrates, neurones communicate to each other by using both spikes and graded potentials. For example, vertebrate photoreceptors and some interneurones in the retina function without spikes (Werblin 1979). Furthermore, some types of interneurones in the vertebrate olfactory bulb have been reported to function without spikes (Shepherd 1981). In invertebrates, some crustacean stretch receptors also function without using spikes (Bush 1981; El Manira et al. 1993) and in arthropod motor control systems, nonspiking local interneurones are important neural elements to organize motor pattern formation. In insects, premotor nonspiking interneurones do not produce spikes but affect the activity of postsynaptic neurones continuously and in a graded way depending on changes in their membrane potential (Burrows 1992).

In the terminal abdominal ganglion of crayfish, two groups of nonspiking local interneurones, the antero-lateral (AL) and postero-lateral (PL) groups, form opposing parallel connections with uropod motor neurones (Nagayama and Hisada 1987; Nagayama et al. 1994; Namba et al. 1994). PL nonspiking interneurones are GABAergic, while many AL interneurones are glutamatergic (Nagayama et al. 1997, 2004). GABA is a common inhibitory neurotransmitter, while glutamate is an excitatory transmitter at crayfish neuromuscular junction, but can act as an inhibitory transmitter in the central nervous system (Nagayama 2005). Simultaneous intracellular recordings between nonspiking interneurones show that most interneurones exhibit one-way inhibitory interactions (Namba and Nagayama 2004). GABAergic one-way inhibitory interactions are also found between locust nonspiking interneurones (Burrows 1992; Wildman et al. 2002).

Although nonspiking interneurones make chemically mediated inhibitory connections with motor neurones in both crayfish and locusts (Burrows 1980; Nagayama et al. 1997), excitatory connections of nonspiking interneurones to motor neurones and/or interneurones within the terminal abdominal ganglion of the crayfish are still unclear. Recently, some nonspiking interneurones in leech and crayfish were reported to make electrical couplings with motor neurones and/or interneurones (Paul and Mulloney 1985; Rodriguez et al. 2009, 2012; Smarandache-Wellmann et al. 2014). To understand this in more detail, we have analyzed the synaptic interactions between nonspiking interneurones and uropod motor neurones using simultaneous intracellular recordings.

Materials and methods

Animals and preparations

Adult male and female crayfish, *Procambarus clarkii* Girard of 7–9 cm in body length, from rostrum to telson, were used for all experiments. They were obtained from a commercial supplier and kept in laboratory tanks with flowing fresh. The abdomen was isolated from the thorax and pinned ventral-side up in a small chamber containing cooled van Harreveld's (1936) solution. The swimmerets were removed and the terminal (sixth) abdominal ganglion exposed by removing the sixth sternite and peeling off the surrounding soft cuticle and the ventral aorta. The terminal ganglion was then stabilized on a silver platform and treated with protease (Sigma type XIV, Sigma St. Louis, MO., USA) for 30 s to soften the ganglionic sheath to aid penetration with glass microelectrodes.

Extracellular recordings

To monitor the activity of uropod motor neurones, the soft cuticle overlying the uropod muscles was removed along the lateral edge of the protopodite and exopodite. The underlying hypodermis, ventral blood vessel, and connective tissue were then removed. A suction electrode was placed over the cut end of either the nerve root 2 or 3 motor bundle. Either the closer, reductor motor neurone (red mn) was recorded at the bifurcation to the reductor and adductor exopodite muscles, or the opener motor neurones were recorded at the bifurcation to the ventral rotator and the abductor exopodite muscles by using suction electrode (Nagayama 1999). The remaining nerve roots were cut or pinched to prevent unwanted inputs.

Simultaneous intracellular recordings

Simultaneous intracellular recordings were carried out from the left half of the terminal ganglion neuropil with glass microelectrodes filled with a 3 % solution of Lucifer yellow CH in 0.1 M lithium chloride (electrode resistance ranged between 100 and 200 MΩ). In some recordings, we used 2 M potassium acetate-filled electrodes (resistance ranged between 30 and 40 MΩ) to observe synaptic events more clearly. The nonspiking local interneurones and the uropod motor neurones were identified physiologically according to the criteria that have been described previously (Nagayama et al. 1984, 1997). The gross morphology of nonspiking interneurones was further confirmed by iontophoretic injection of Lucifer Yellow using 1–3 nA hyperpolarizing current pulses of 500 ms duration at 1 Hz for 3–5 min. Dual-channel bioelectric amplifiers (MEG-2100, NIHON KOHDEN, Japan) were used for extracellular recordings, and 2 microelectrode amplifiers (MEZ-8201, NIHON KOHDEN, Japan) were used for intracellular recordings and staining. All physiological recordings were stored on a PCM data recording systems for later analysis and displayed on a digital scope which sample rate was 10 MS/s (DL708E, Yokogawa, Japan). The results are based on 26 pairs of successful simultaneous intracellular recordings from 73 crayfish.

Results

Results from twenty-six pairs of stable simultaneous intracellular recordings between nonspiking local interneurones and uropod motor neurones were obtained. One nonspiking interneurone had no effect on the motor neurones, 17 interneurones made inhibitory connections, and remaining eight interneurones made excitatory connections with the uropod motor neurones. We will show here only briefly the
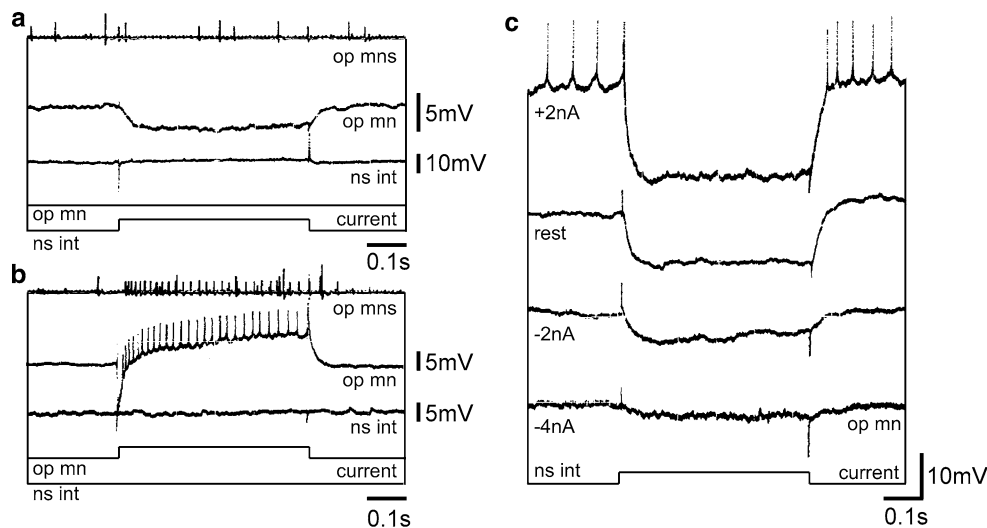
Fig. 1 Inhibitory connection of nonspiking interneurone on an opener motor neurone. **a** A 1 nA depolarizing current injected into the nonspiking interneurone hyperpolarized the opener motor neurone. **b** A 3 nA depolarizing current injected into the motor neurone caused a train of spikes in the motor neurone, but had no effect on the membrane potential of the nonspiking interneurone. **c** Depolarization of the motor neurone with +2 nA increased the amplitude of the nonspiking interneurone-mediated membrane hyperpolarization, while the hyperpolarizing the motor neurone with −2 and −4 nA decreased this effect

inhibitory interactions between nonspiking interneurones and the uropod motor neurones, since we reported previously that they are chemically mediated (Nagayama et al. 1997) and will focus in this paper on the excitatory connections of the nonspiking interneurones.

Inhibitory connections between nonspiking interneurones and motor neurones

Figure 1 shows a typical inhibitory connection from a nonspiking interneurone to a uropod motor neurone. Depolarizing current (+1 nA) injected into the nonspiking interneurone (ns int in Fig. 1a) hyperpolarized the slow opener motor neurone (op mn in Fig. 1a). On the other hand, a train of spikes of the opener motor neurone elicited by injection of a + 3 nA depolarizing current pulse caused no significant change in the membrane potential of the nonspiking interneurone (Fig. 1b). The postsynaptic inhibition of the motor neurone, mediated by the inhibitory synapse when the nonspiking interneurone was depolarized, increased when the motor neurones were depolarized continuously and decreased when the motor neurones were hyperpolarized (Fig. 1c). This suggests that there is a typical chemical synapse from the nonspiking interneurone to the motor neurone. The spiking activity of the motor neurones had no postsynaptic effects on the membrane potential of the nonspiking interneurones, in all 17 recordings. In five out of 17 recordings, hyperpolarizing the nonspiking interneurones depolarized the uropod motor neurones which suggested

that the nonspiking interneurones continuously released inhibitory transmitter at their resting potential.

One-way excitatory connections from nonspiking interneurones to slow motor neurones

In eight paired recordings, we found nonspiking interneurones made excitatory connections with the uropod motor neurones. In four of these pairs, the interaction was one-way (or unidirectional) showing that nonspiking interneurones excited directly the motor neurones. All these four recorded motor neurones were tonically active slow motor neurones. For example, a depolarizing current (+1 nA) injected into the PL type nonspiking interneurone depolarized the closer, reductor motor neurone and increased its spike frequency (Fig. 2a). Hyperpolarizing current (−1 nA) injected into the nonspiking interneurone hyperpolarized the motor neurone and decreased its spike discharge (Fig. 2b). When the membrane potential of the reductor motor neurone was depolarized with a + 1 nA current injection, it increased its frequency but had no obvious effect on the membrane potential of the nonspiking interneurone (Fig. 2c). In another preparation (Fig. 2d), hyperpolarization of the reductor motor neurone with a −1 nA current injection decreased the amplitude of the nonspiking interneurone-mediated membrane depolarization. This would be unusual if the effect was mediated by chemical synaptic transmission.
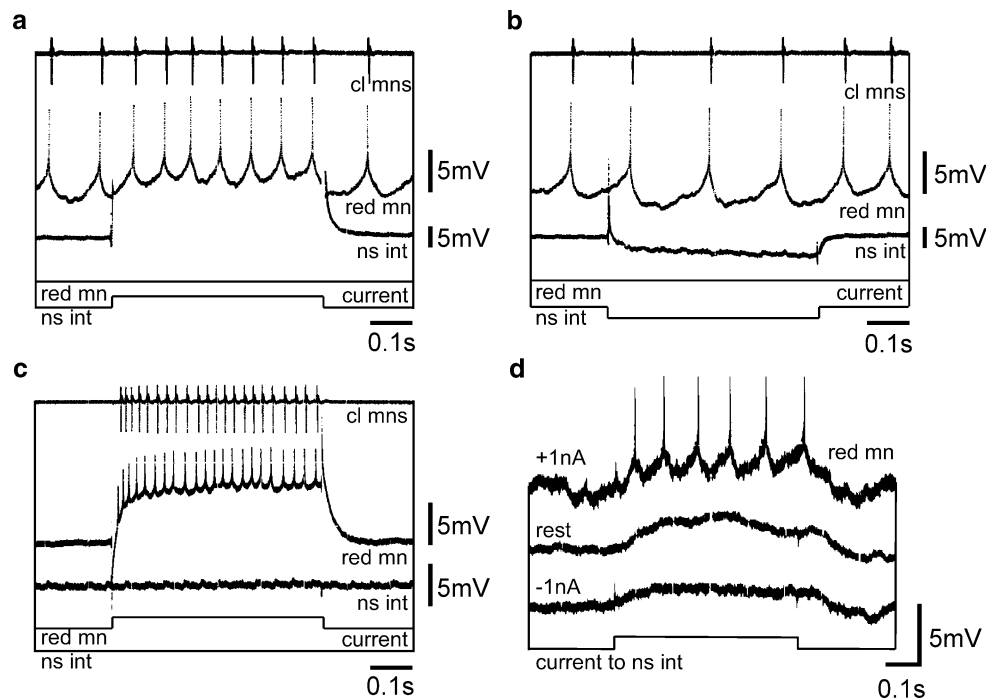
Fig. 2 Excitatory connection of nonspiking interneurone on the closer reductor motor neurone. **a** A 1 nA depolarizing current injected into the PL type nonspiking interneurone depolarized the reductor motor neurone and increased its spike discharge. **b** A 1 nA hyperpolarizing current injected into the nonspiking interneurone hyperpolarized the motor neurone and decreased its spike discharge. **c** Depolarization of the motor neurone with +1 nA caused a train of its spikes, but had no effect on the membrane potential of the non-spiking interneurone. **d** Depolarization of the motor neurone with +1 nA increased the amplitude of the nonspiking interneurone-mediated membrane depolarization, while hyperpolarizing the motor neurone with −1 nA decreased this effect. **a**–**d** are from different preparations

Bidirectional excitatory connections between nonspiking interneurones and fast motor neurones

Motor neurones also made output effect on nonspiking interneurones in the remaining four pairs of excitatory connections between nonspiking interneurone and motor neurones. In all cases, the motor neurones were fast lateral abductor exopodite and dorsal rotator motor neurones. Depolarizing current (+5 nA) injected into a nonspiking interneurone depolarized the fast opener, the lateral abductor motor neurone (Fig. 3a). The motor neurone was spiked, in advance, with +4 nA depolarizing current. The membrane of the nonspiking interneurone was also depolarized when +5 nA depolarizing current was injected into the motor neurone (Fig. 3b). Small discrete depolarizations following spikes of the motor neurone were also observed in the nonspiking interneurone (asterisks in Fig. 3b). Nonspiking interneurone-mediated membrane depolarization of the motor neurones was increased in amplitude by about 30 % when 3 nA depolarizing current was injected into the motor neurone, while it was decreased by about 10 % when 3 nA hyperpolarizing current was injected into the motor neurone (Fig. 3c). The amplitude of the tonic excitatory

postsynaptic potentials (EPSPs) in the motor neurone was, however, decreased by depolarization and increased by hyperpolarization (Fig. 3c).

The dorsal rotator motor neurone has a cell body of about 40 μm in diameter located at the ventral surface of the antero-medial portion of the terminal ganglion (Fig. 4a). The motor neurone extends its main dendrites in an arch both antero-medially and postero-medially, and its axon enters nerve root 1. Depolarizing current (+2 nA) injected into the AL-II type nonspiking interneurone (e.g., Nagayama et al. 1997) depolarized with a train of spikes in this motor neurone (Fig. 4b). Depolarizing current (+2 nA) injected into the dorsal rotator motor neurone also caused a sustained membrane depolarization of the nonspiking interneurone (Fig. 4c). Each motor neurone spike elicited a one to one EPSP in the nonspiking interneurone with a very short delay of 0.2 ms (Fig. 4d).
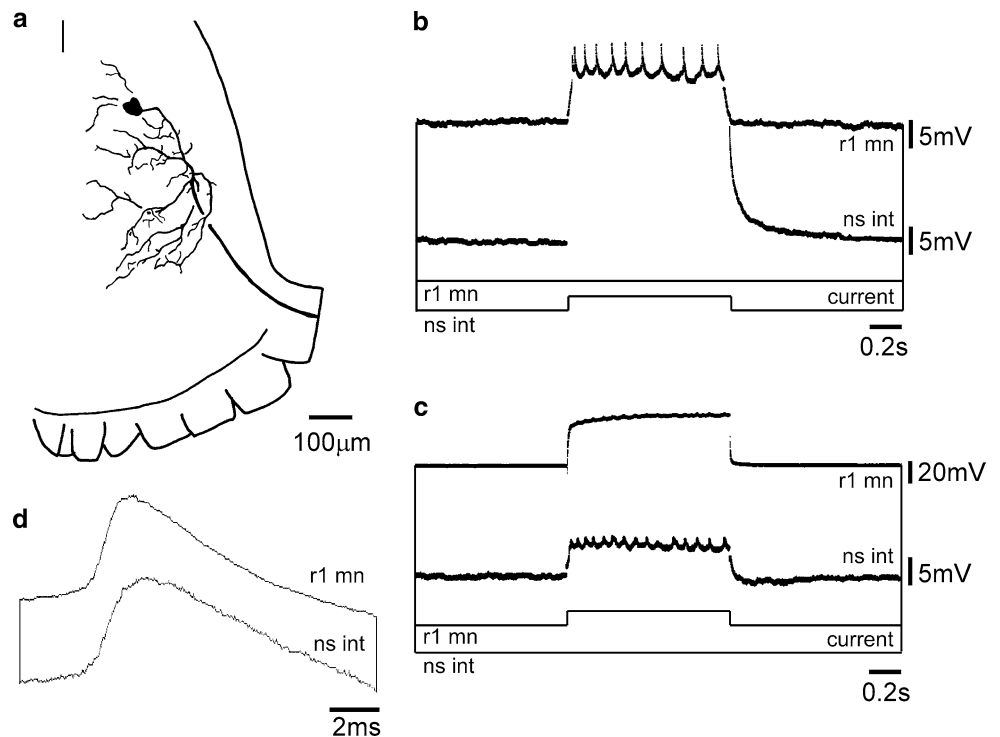
The AL-III type nonspiking interneurone (e.g., Nagayama et al. 1997) also had bidirectional excitatory connections with the dorsal rotator motor neurone (Fig. 5). A 3 nA depolarizing current injected into the nonspiking interneurone depolarized the motor neurone of about 15 mV in amplitude (Fig. 5a, left). This nonspiking interneurone-mediated membrane depolarization was changed little by injection
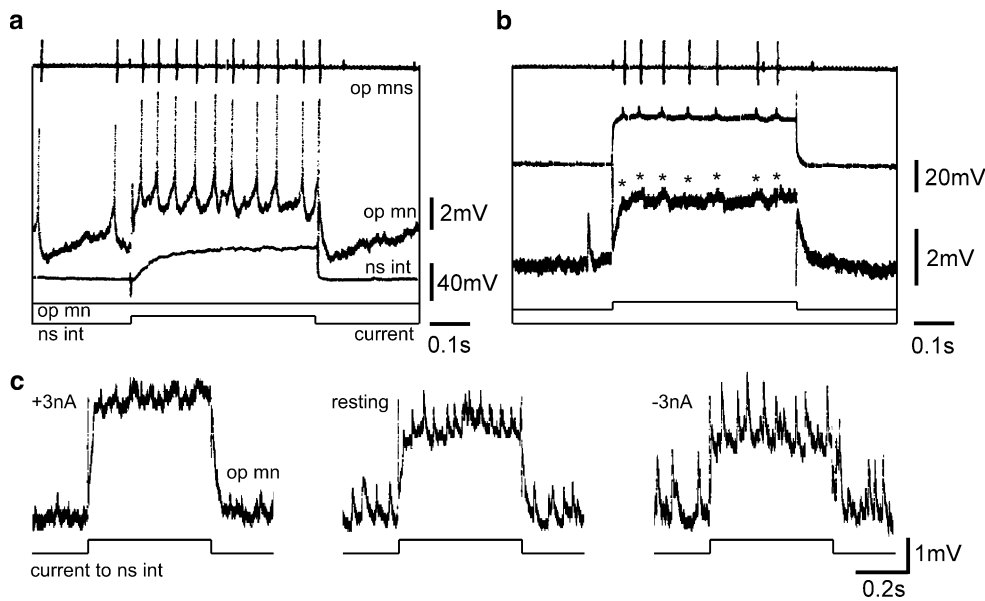
Fig. 3 Excitatory connection of a nonspiking interneurone on a fast opener motor neurone. **a** A 5 nA depolarizing current injected into the nonspiking interneurone depolarized the fast opener, lateral abductor exopodite motor neurone. This motor neurone spiked in advance by +4 nA depolarizing current injection. **b** A 5 nA depolarizing current injected into the motor neurone depolarized the nonspiking interneurone. Asterisks indicate discrete EPSPs that were followed by motor neurone spikes. **c** Depolarization of the motor neurone with +3 nA increased the amplitude of the nonspiking interneurone-mediated membrane depolarization, while hyperpolarizing the motor neurone with −3 nA decreased this effect. Note that the amplitudes of the tonic EPSPs of the motor neurone were decreased by depolarizing current injection into the motor neurone, while they were increased by hyperpolarizing current injection

Fig. 4 Excitatory connection of nonspiking interneurone on the fast dorsal rotator motor neurone. **a** Morphology of the dorsal rotator motor neurone. Anterior at the top. **b** A 2 nA depolarizing current injected into the nonspiking interneurone depolarized the dorsal rotator motor neurone and elicited a train of spikes. **c** A 2 nA depolarizing current injected into the motor neurone depolarized the nonspiking interneurone. Note that discrete EPSPs were followed by motor neurone spikes. **d** Signal averaged records (128 sweeps) triggered from spikes of the motor neurone showed a very short latency of direct excitatory connection with the nonspiking interneurone

of hyperpolarizing current (−1 nA) into the motor neurone (Fig. 5a, right). A 5 nA hyperpolarizing current injected into the nonspiking interneurone hyperpolarized the motor neurone of about 5 mV in amplitude (Fig. 5b, left). This amplitude was not changed significantly when the motor neurone was hyperpolarized (Fig. 5b, right). Depolarizing

Fig. 5 Bidirectional excitatory connection between the dorsal rotator motor neurone and a nonspiking interneurone. Left, with no hyperpolarizing current injected into the motor neurone, and right, with 1 nA hyperpolarizing current injected into the motor neurone in advance. **a** A 3 nA depolarizing current injected into the nonspiking interneurone depolarized the motor neurone. **b** A 5 nA hyperpolarizing current injected into the nonspiking interneurone hyperpolarized the motor neurone. **c** A 3 nA depolarizing current injected into the motor neurone depolarized the nonspiking interneurone. **d** A 5 nA hyperpolarizing current injected into the motor neurone hyperpolarized the nonspiking interneurone
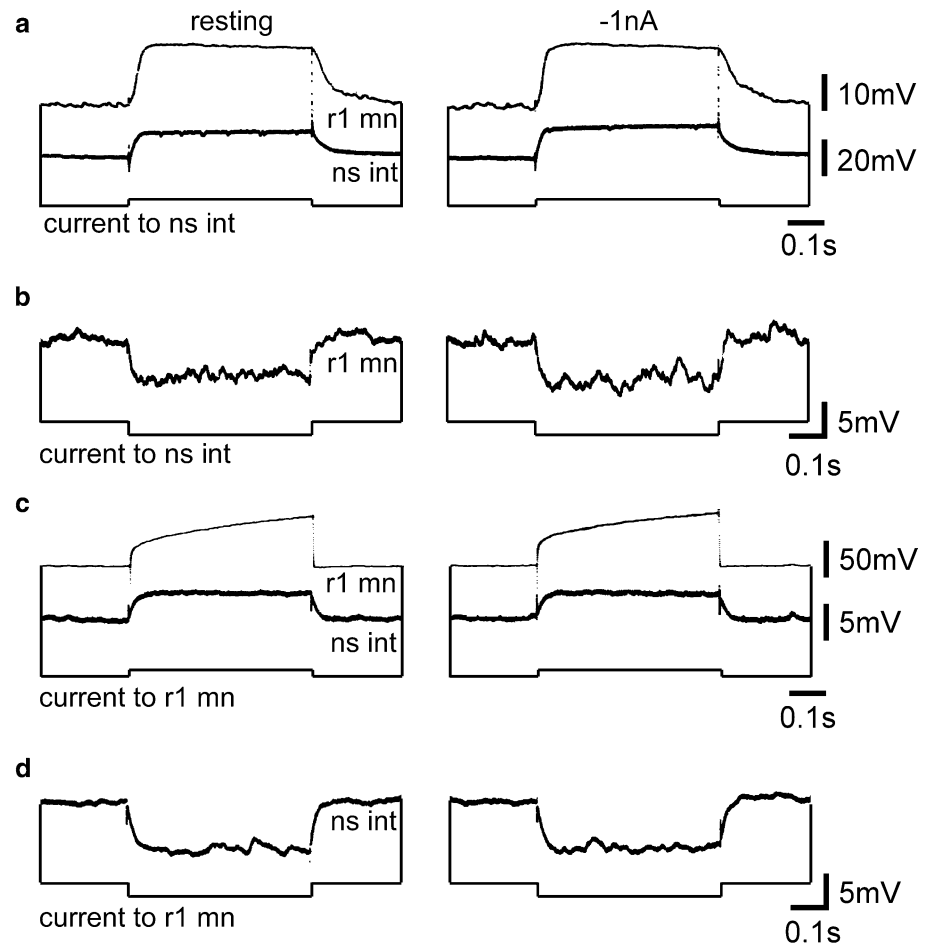
current (+3 nA) injected into the motor neurone depolarized the nonspiking interneurone. The amplitude of this sustained depolarization was changed little when the nonspiking interneurone was hyperpolarized by −1 nA current injection (Fig. 5c). Hyperpolarization of the motor neurone (−5 nA) hyperpolarized the nonspiking interneurone (Fig. 5d, left). Again, the amplitude was not changed significantly by manipulation of nonspiking interneurone membrane (Fig. 5d, right). The depolarizing current injection into the motor neurone also had no significant effect on the amplitude of the nonspiking interneurone-mediated membrane potential change, and vice verse (not shown).

One nonspiking interneurone had both excitatory and inhibitory synapses

As we have reported previously (Namba and Nagayama 2004), some nonspiking interneurones make direct inhibitory or excitatory connections with other nonspiking interneurones. In this study, we found one particular AL-III type nonspiking interneurone which made both inhibitory and excitatory connections with other nonspiking interneurones (Fig. 6). Depolarizing current (+5 nA) injected into this

interneurone (ns int 1 in Fig. 6) hyperpolarized the second AL-III type nonspiking interneurone (ns int2) with a decrease in spike discharge of the opener motor neurones (Fig. 6a). Depolarizing currents injected into ns int2 had no effect upon the membrane potential of the first interneurone (ns int1). After this recording, the second microelectrode was moved and penetrated a third AL-III nonspiking interneurone (ns int3). Depolarizing current of 5 nA injected into the first interneurone (ns int1) depolarized the third nonspiking interneurone (ns int3) and the opener motor neurones decreased their activity (Fig. 6b). Injection of +6 nA depolarizing current into ns int3 depolarized ns int1 (Fig. 6c). Thus, the first nonspiking interneurone (ns int1) had inhibitory connections to the second nonspiking interneurone (ns int2) and, simultaneously, excited the third nonspiking interneurone (ns int3). The inhibitory interaction was one-way but the excitatory interactions were bidirectional.

Discussion

We showed in this study that inhibitory connections between nonspiking interneurones and uropod motor

Fig. 6 Inhibitory and excitatory connections of a nonspiking interneurone. **a** A 5 nA depolarizing current injected into the nonspiking interneurone (ns int1) hyperpolarized the second nonspiking interneurone (ns int2) and decreased the spike discharge of the opener motor neurones. **b** A 5 nA depolarizing current injected into ns int1 depolarized the third nonspiking interneurone (ns int3) with a decrease in the motor neurone spikes. **c** A 6 nA depolarizing current injected into ns int3 depolarized the ns int1. Inset shows a schematic of the connections among the nonspiking interneurones
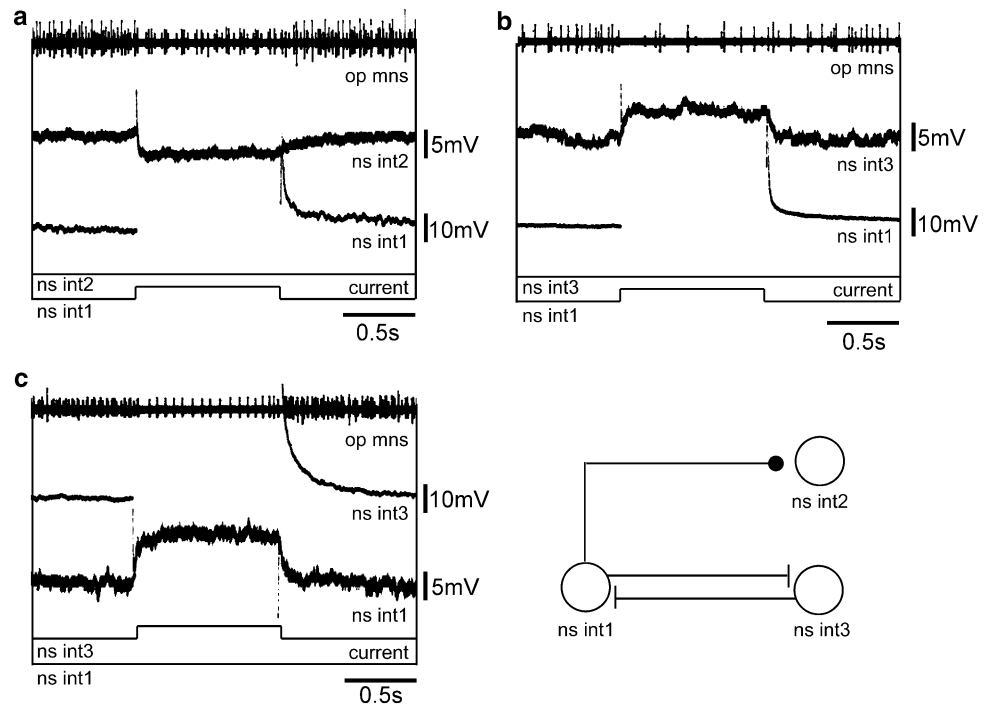
neurones were mediated by chemical synapses. We also found that excitatory connections between them were not simply mediated by classical chemical synapse but instead were mediated by electrical synapse. Excitatory connections were one-way in the case of slow motor neurones while bidirectional with fast motor neurones.

Nonspiking interneurones excite uropod motor neurones

In contrast to the inhibitory interactions (Nagayama et al. 1997; Namba and Nagayama 2004), the excitatory connections between nonspiking interneurones and motor neurones were not likely to be mediated by typical chemical synapses but instead through electrical synapses. In some preparations, a steady hyperpolarizing or depolarizing current injected into the motor neurones had no effect upon the amplitude of nonspiking interneurones-mediated membrane potential change (three out of eight recordings). This is the case in the synaptic connections from chordotonal afferents to the lateral giant interneurones (LGs) that are mediated by electrical synapses. The amplitude of the afferent-mediated EPSPs of the LGs is not changed by voltage manipulation of the LGs and by the exchange of external solution from normal saline to Ca^{++}-free solution (Newland et al. 1997). In remaining preparations in this study (five out of eight recordings), a steady depolarizing current injected into the motor neurone increased the amplitude of the nonspiking interneurone-mediated membrane depolarization, whereas hyperpolarizing current decreased it. These

voltage-dependent changes of electrical coupling are generally attributed to voltage-dependent properties of the gap junction channels (Furshpan and Potter 1959; Heitler et al. 1991; Pereda et al. 1995; Curti and Pereda 2004). A very short latency of about 0.2 ms from the onset of spikes in dorsal rotator motor neurone to the onset of EPSPs in the nonspiking interneurone also supports the notion that there was electrical coupling between them. Further confirmation of dye-coupling using neurobiotin staining (e.g., Antonsen and Edwards 2003; Haag and Borst 2005; Fan et al. 2005; Smarandache-Wellmann et al. 2014) would have clarified this point.

Nonspiking interneurones inhibit uropod motor neurones

The nonspiking interneurone-mediated membrane hyperpolarization of the uropod motor neurones was decreased and reversed in amplitude by steady hyperpolarizing current injected into the motor neurones. The inhibitory connections with the motor neurones were chemically mediated synaptic transmission in a similar fashion to the inhibitory connections between nonspiking interneurones themselves (Namba and Nagayama 2004). Immunocytochemical studies have indicated that many nonspiking interneurones, especially PL interneurones, are GABAergic (Nagayama et al. 1997) and some AL interneurones are glutamatergic (Nagayama et al. 2004). GABA is the most widely distributed inhibitory neurotransmitter in both vertebrates and invertebrates (e.g., Takeuchi and Takeuchi 1965) and

in the crustacean central nervous system. Glutamate also functions as an inhibitory transmitter (e.g., Marder 1987; Nagayama 2005).

Two types of electrical synapses

In crayfish swimmeret system, some nonspiking interneurones have been shown to make electrical coupling with swimmeret motor neurones and local commissural interneurones (Paul and Mulloney 1985; Smarandache-Wellmann et al. 2014). Furthermore, leech premotor nonspiking interneurones are coupled with excitatory motor neurones (Rela and Szczupak 2003; Rodriguez et al. 2009, 2012). The connections are one-way and nonspiking interneurones are coupled through electrical junctions to motor neurones. In this study, excitatory connections of nonspiking interneurones to slow motor neurones were one-way, while the connections with fast motor neurones were non-rectifying bidirectional. The uropods are the last abdominal appendages, and the closing and opening of the uropods are responsible for equilibrium reactions, avoidance reactions, and tailflips (Nagayama et al. 1986, 2002). The slow uropod motor neurones fire tonically and control the continuous movements of the uropods during walking, while the fast motor neurones are usually silent and fire during rapid fast movements of the abdomen during tailflipping (Nagayama et al. 2002). Though the slow motor neurones were activated by the nonspiking interneurones, fast motor neurones activity was usually a subthreshold, membrane depolarization. Furthermore, we did not find any inhibitory outputs of nonspiking interneurones to fast motor neurones, but all 17 successful recordings demonstrated inhibitory outputs to slow motor neurones. Thus, nonspiking interneurones directly control the organization of slow motor neurone activity, while they appear to regulate the background activity of the fast motor neurones.

One nonspiking interneurone has reciprocal excitatory and inhibitory connections

Many nonspiking interneurones have reciprocal output effects upon antagonistic motor neurone (Nagayama et al. 1984). Depolarizing current injected into the nonspiking interneurone decreases spike activity of slow closer motor neurones and increases that of antagonistic slow opener motor neurones. Though many nonspiking interneurones release inhibitory transmitters of GABA or glutamate (Nagayama et al. 1997, 2004; Nagayama 2005), we have shown previously that a disinhibitory pathway from nonspiking interneurones through connections via other nonspiking interneurones is responsible for excitation of certain motor neurones (Namba and Nagayama 2004). In this study, we showed that electrical couplings with motor neurones are another excitatory outputs of nonspiking interneurones.

Both PL and AL nonspiking interneurones were found to make electrical couplings with the motor neurones suggesting that certain nonspiking interneurones may make inhibitory connections with motor neurone via chemically mediated synapse on specific branches. At the same time, they may make excitatory connections with antagonistic motor neurone via electrical couplings on other branches. At the moment, there is no direct evidence to support this hypothesis, but we have demonstrated in this study that one particular nonspiking interneurone has both excitatory and inhibitory synapses simultaneously to different nonspiking interneurones. Since the number of central neurones of arthropods is limited, multifunctional nonspiking interneurones would allow for the generation of complex movements combined with economy.

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