

Calcium waves

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Waves through living systems are best characterized by their speeds at 20°C. These speeds vary from those of calcium action potentials to those of ultraslow ones which move at 1–10 and/or 10–20 nm s⁻¹. All such waves are known or inferred to be calcium waves. The two classes of calcium waves which include ones with important morphogenetic effects are slow waves that move at 0.2–2 µm s⁻¹ and ultraslow ones. Both may be propagated by cycles in which the entry of calcium through the plasma membrane induces subsurface contraction. This contraction opens nearby stretch-sensitive calcium channels. Calcium entry through these channels propagates the calcium wave. Many slow waves are seen as waves of indentation. Some are considered to act via cellular peristalsis; for example, those which seem to drive the germ plasm to the vegetal pole of the *Xenopus* egg. Other good examples of morphogenetic slow waves are ones through fertilizing maize eggs, through developing barnacle eggs and through axolotl embryos during neural induction. Good examples of ultraslow morphogenetic waves are ones during inversion in developing *Volvox* embryos and across developing *Drosophila* eye discs. Morphogenetic waves may be best pursued by imaging their calcium with aequorins.

Keywords: calcium waves; morphogenesis; stretch-sensitive channels; peristalsis; aequorin

1. INTRODUCTION

Calcium waves were discovered as the wave of elevated free cytosolic calcium which traverses medaka fish eggs during fertilization (Gilkey *et al.* 1978; figure 1). This wave moves at approximately 10 µm s⁻¹ as do all fertilization waves when corrected for temperature. Fertilization waves, in turn, are part of the group of calcium waves called fast ones that move at 10–30 µm s⁻¹ through cells (Jaffe 2002) and are propagated along endoplasmic reticula to bring about ‘calcium-induced calcium release’ from its interior (Jaffe 1991). Fast calcium waves, in turn, are one of 4–5 groups of calcium waves when these are arranged by propagation speed (figure 2).

Since this paper is based on a lecture given at a recent Royal Society meeting on ‘Calcium signals and developmental patterning’, the main focus will be on slow and ultraslow calcium waves, the only groups that much effect such patterning. All speeds are corrected for temperature via Cosens *et al.* (1976). According to Cosens *et al.*, transport speeds fell by nearly fivefold as the temperature fell from 38 to 20°C and nearly doubled when the temperature rose from 14 to 20°C—a clear indicator that temperature corrections are needed. This could surely be improved by using reports of temperature dependence that are appropriate for the particular process considered rather than a single one; however, time does not allow this now. More important, it should be emphasized that many papers do not mention speeds in the text; in these papers, speeds were obtained from images of the

process involved. For example, the speed of the indentation wave along barnacle eggs was obtained from the length and time data shown in figure 1 of Lewis *et al.* (1973).

2. SLOW CALCIUM WAVES

Table 1 shows a list of 28 cases of slow waves which were selected from approximately 60 reports by listing only what seem to be the most reliable ones in those cases where measurements of essentially the same wave speed were reported in different papers. Seven of these were directly seen to be calcium waves while in the eighth (no. 13 that accompanies the fertilization of maize eggs) a 1 µm s⁻¹ wave of calcium influx was observed. The fertilization wave through maize eggs is of special interest since it travels far more slowly than those through animal eggs. This may have evolved since the equivalent of polyspermy cannot occur in maize eggs which would allow the evolution of a slower and perhaps less expensive mechanism.

More important, this list confirms that calcium waves that move at 0.2–2 µm s⁻¹ form a natural group as was proposed by Jaffe & Créton (1998) and is shown in figure 2, while figures 3–5 show three examples of such slow waves, namely ones through maize eggs during fertilization, through postfertilization barnacle eggs and through axolotl embryos during neural induction.

Proposed mechanisms for the propagation of slow intracellular and intercellular calcium waves are shown in figures 6 and 7, respectively. The proposed intracellular mechanism may be thought to start with the entry of calcium ions through a stretch-sensitive channel. The resultant rise in the concentration of subsurface calcium induces the contraction of

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One contribution of 11 to a Discussion Meeting Issue ‘Calcium signals and developmental patterning’.

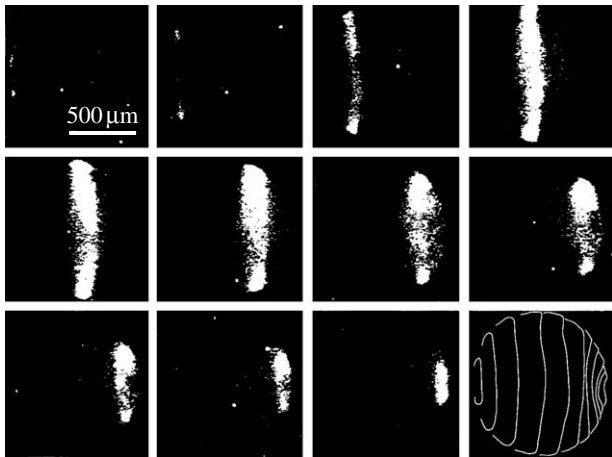


Figure 1. A calcium wave through a fertilizing medaka egg. Adapted from Gilkey *et al.* (1978, fig. 2a).

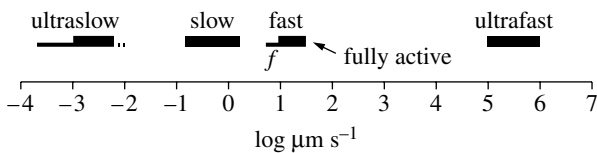


Figure 2. The speeds of groups of calcium waves: *f* means fertilization. Modified from Jaffe & Créton (1998, fig. 2).

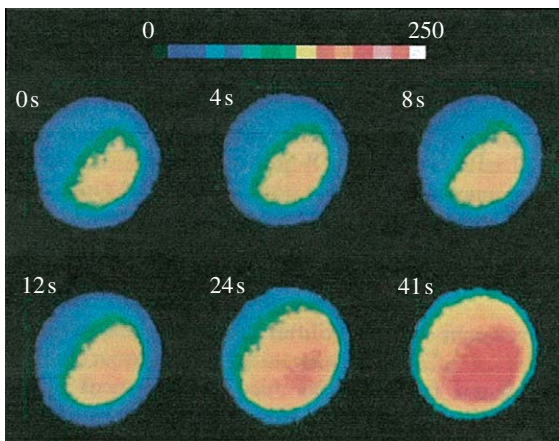


Figure 3. A calcium wave through a fertilizing maize egg. Adapted from Digonnet *et al.* (1997, fig. 3A).

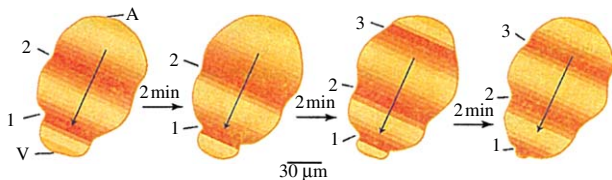


Figure 4. A 'peristaltic' postfertilization wave through a barnacle egg: A, animal pole; V, vegetal pole. Adapted from Jaffe (1999, fig. 6B).

actinomyosin filaments similar to those induced to contract by calcium increases in muscle cells. This contraction relays the calcium wave by opening nearby stretch-sensitive calcium channels. These then let in calcium to propagate the cycle. The proposed mechanism for intercellular calcium waves inserts a

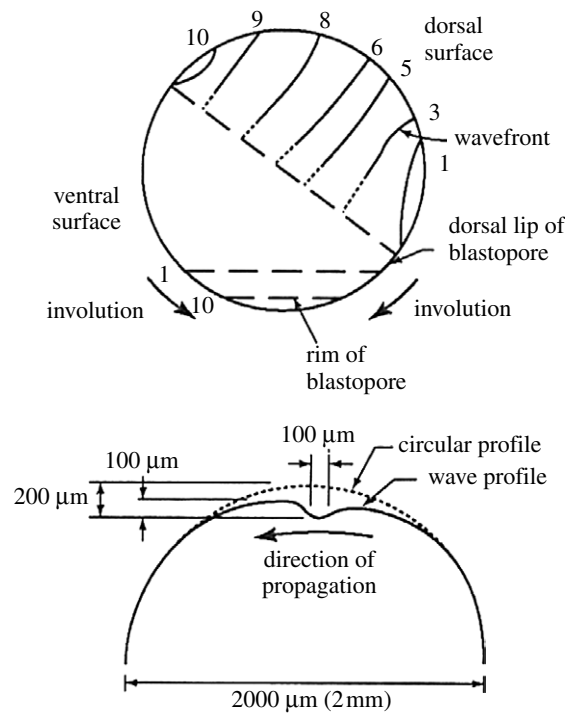


Figure 5. A wave across an axolotl embryo during neurulation. Adapted from Jaffe (1999, fig. 6C).

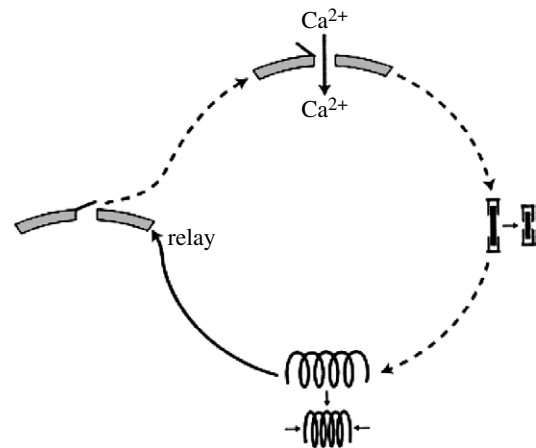


Figure 6. A proposed mechanism for the propagation of slow intracellular calcium waves.

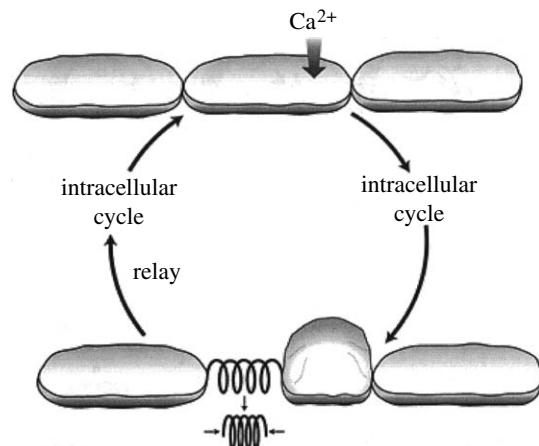


Figure 7. A proposed mechanism for the propagation of slow intercellular calcium waves.

Table 1. A selected list of speeds of slow waves.

no.	system	indicator	speed ($\mu\text{m s}^{-1}$)
<i>eggs</i>			
1	<i>Beröe</i> (Ctenophore; Houliston <i>et al.</i> 1993)	'peristaltic' indentation	~0.2
2	leech (Fernandez <i>et al.</i> 1990)	indentation	1.0
3	barnacle (Lewis <i>et al.</i> 1973; fig. 4B)	indentation	0.4
4	cricket (Vollmar 1972)	'peristaltic' indentation	0.4
5	gall midge (Wolf 1985)	particle saltation	0.3
6	ascidian (Sardet <i>et al.</i> 1989)	indentation	1.4
7	medaka fish (Fluck <i>et al.</i> 1991)	calcium and indentation	1.5
8	zebrafish (Créton <i>et al.</i> 1998)	calcium via aequorin	0.5
9	<i>Xenopus</i> (Savage & Danilchik 1993)	'peristaltic' indentation	0.5
10	toad (Dan 1960)	indentation	0.6
11	newt (Selman & Waddington 1955)	indentation	1.4
12	<i>Xenopus</i> (Muto <i>et al.</i> 1996)	calcium and indentation	1.8
13	maize (Antoine <i>et al.</i> 2000, fig. 3)	calcium influx	1.1
<i>later in development</i>			
14	weevil (Miyamoto & van der Meer 1982)	yolk contraction	0.2
15	blowfly (Agrell 1962)	mitosis	0.8
16	<i>Drosophila</i> (Foe & Alberts 1983)	mitosis	0.4
17	<i>Drosophila</i> (Kam <i>et al.</i> 1991)	ingression	0.2
18	medaka's stellate layer (Simon & Cooper 1995)	calcium	0.3
19	chick embryo (Stern & Goodwin 1977)	cell movement	0.7
20	chick embryo (Robertson 1979)	cell movement	
	parallel to somites	refractive index	0.7
	perpendicular to somites	refractive index	0.3
<i>other</i>			
21	<i>Dictyostelium</i> 's mound formation (Rietdorf <i>et al.</i> 1996)	optical density ^a	1.1
22	<i>Dictyostelium</i> 's slug (Dormann & Weijer 2001)	optical density ^a	0.7
23	isolated <i>Dictyostelium</i> cells (Bretschneider <i>et al.</i> 2004)	actin polymerization	0.7
24	two-dimensional <i>Dictyostelium</i> slugs ^b (Rieu <i>et al.</i> 2004)	autofluorescence	1.0
25	hydroid polyps (Belousov <i>et al.</i> 1989)	cell reorientation	1.0
27	moss filaments (Tucker <i>et al.</i> 2005)	calcium	2.0
28	lily pollen (Malhó & Trewavas 1996)	calcium	0.6

^a It was argued by Jaffe (1997) that these waves of optical density are the ones of surface cell contraction which would stretch surface cells (and hence their membranes) in nearby zones along the direction of wave movement.

^b These two-dimensional slugs are one cell thick, yet behave like natural slugs that are many cells thick (Bonner 1998).

new step in each cycle in which a wave through one cell induces it to round up and in this way tug on and stretch the nearest stretch-sensitive channels in adjacent cells. It has been suggested that waves of such changes in cell shape accompany optical density waves along *Dictyostelium* slugs (Jaffe 1997). This conjecture was based upon the facts that postaggregation cells in *Dictyostelium* rounded up or 'cringed' soon after cyclic AMP was applied to them (Futrelle *et al.* 1982) and that cyclic AMP waves are believed to accompany optical density waves in *Dictyostelium* slugs (Dormann & Weijer 2001).

One important function of slow waves may be to drive materials towards one pole of a cell via peristalsis and this process is shown in figure 8. Cases in which this is believed to occur are listed in table 1. These include case no. 1 (that of *Beröe* eggs), case no. 4 (that of cricket eggs) and case no. 9 (that of *Xenopus embryos*).

3. ULTRASLOW WAVES

A list of ultraslow waves that may be morphogenetic is shown in table 2. While calcium has never been imaged during an ultraslow wave, one can infer from the following evidence that they are calcium waves and that

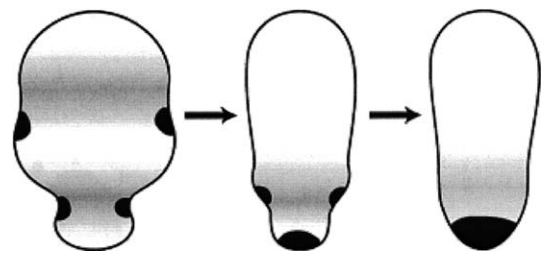


Figure 8. Diagrammatic representation of how cell peristalsis can drive intracellular material towards one pole of a cell.

they are driven by the same mechanisms that propagate slow waves.

Re. the inversion of developing *Volvox* embryos (figure 9), Kelland (1977) pointed out that this process involves a wave of contraction of almost all of its cells at their basal ends. Since localized contraction is well known to be effected by increases in calcium which act on actomyosin, this old observation alone strongly suggests that inversion is effected by a calcium wave. Moreover, actomyosin inhibitors were found to inhibit inversion (Nishii & Ogihara 1999), and Nishii *et al.* (2003) showed that a particular kinesin is needed for inversion while others have shown that calcium regulates some kinesins.

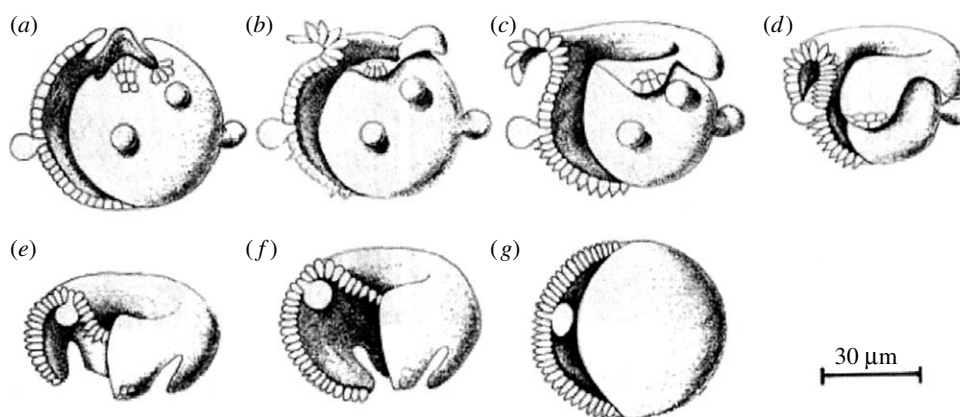


Figure 9. Inversion of developing *Volvox* embryos. Adapted from Kelland (1977, fig. 2).

Re. the ultraslow waves of furrowing seen in developing *Drosophila* eye discs (figure 10) and in developing amphibian embryos: waves of furrowing are waves of indentation during cell division and 10 of the cases of slow waves listed in table 1 are seen as indentation waves.

Re. the DNA replication waves seen in the *Euplotes* macronucleus (figure 11): isolated macronuclei of *Euplotes* are reported to reversibly and grossly contract as calcium is raised in the physiological range (Arikawa *et al.* 2003). This surprising finding suggests the possibility of an ultraslow calcium wave deep within a cell.

Re. the waves of growth cone formation or 'sprouting' along embryonic hippocampal neurons (figure 12): Tam & Gordon (2003) have reviewed evidence in the neuromuscular junction that an influx of calcium ions is needed for sprouting.

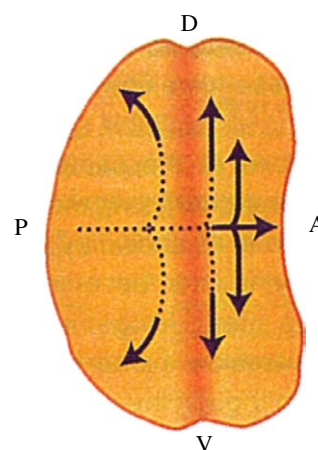


Figure 10. Pattern formation in the developing eye disc in *Drosophila*: D, dorsal; V, ventral; A, anterior; P, posterior. Adapted from Jaffe (1999, fig. 5A).

4. CONCLUSIONS

The main conclusions are the following:

- (i) the first thing that one should know about a wave is its speed,
- (ii) all waves are known or inferred to be calcium waves,
- (iii) slow and ultraslow calcium waves are the most important ones for pattern generation, and
- (iv) slow and ultraslow calcium waves may be mechanically propagated by travelling cycles that involve stretch-activated calcium channels.

The pursuit of calcium waves most needs investigations of calcium patterns within waves, and this would be best done with the luminescent aequorins rather with fluorescent calcium indicators. The advantages of imaging calcium patterns with aequorins are presented in Créton *et al.* (1999) and include: imaging with aequorins is not disturbed by the exciting light that is needed to use fluorescent indicators; it allows continuous recording for periods of more than a day; it provides quantifiable output over the whole physiological range of calcium concentrations. Aequorins (or really apoaequorins) can be introduced by transfection as well as injection. This allows study throughout the organism's life as well as those of its female progeny. Moreover, slow and ultraslow waves

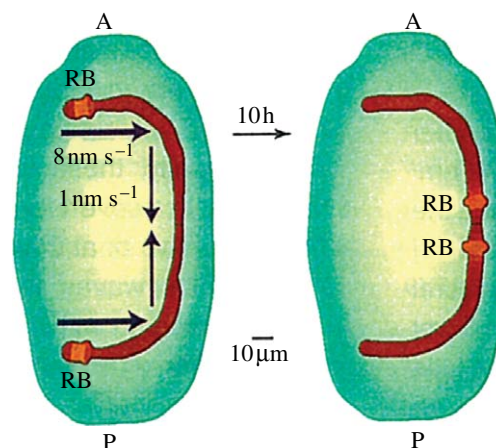


Figure 11. Movement of the DNA replication band (RB) along the macronucleus of the developing ciliate, *Euplotes*: A, anterior; P, posterior. Adapted from Jaffe (1999, fig. 5B).

move so slowly that high spatial resolution can be exchanged for low temporal resolution in *their* study with aequorins.

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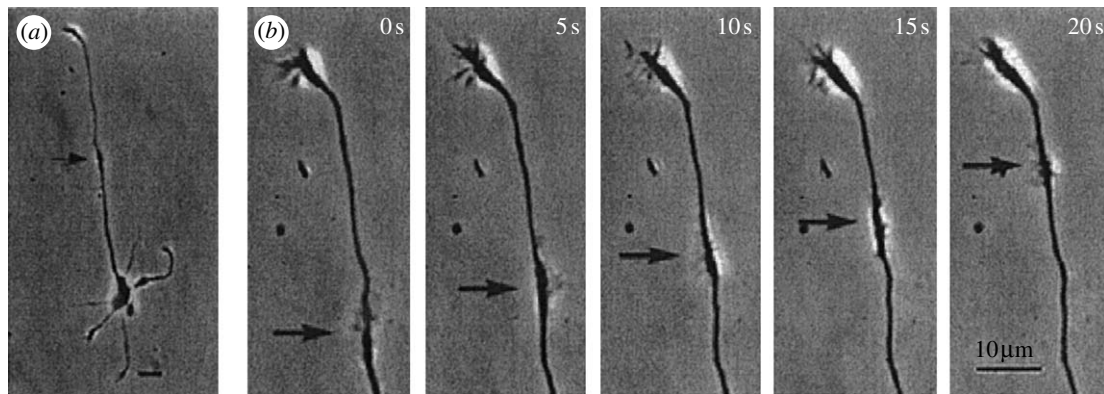


Figure 12. Wave of protrusion of a structure that resembles a growth cone that was recently isolated from embryonic rat hippocampi. Adapted from Ruthel & Banker (1998, fig. 1b).

Table 2. A list of ultraslow waves that may be morphogenetic. (Note that these speeds are in nm s^{-1} rather than $\mu\text{m s}^{-1}$.)

no	system	indicator	speed (nm s^{-1})
1	<i>Candida albicans</i> (Dujardin & Walbaum 1985)	spore formation	8
2	<i>Volvox Roussetii</i> (Pockock 1933)	inversion	10
3	<i>V. aureus</i> (Kelland 1977, fig. 9)	inversion	10
4	<i>V. carteri</i> ^a (Viamontes & Kirk 1977)	inversion	15
5	<i>Drosophila</i> eye disc (Tio <i>et al.</i> 1996)	furrowing forward	1
	<i>Drosophila</i> eye disc (Tio <i>et al.</i> 1996)	furrowing sideways	6
6	axolotl embryo (Brodland <i>et al.</i> 1994)	furrowing during neural induction	50
7	axolotl embryo (Armstrong & Graveson 1988), figure 5	somite segmentation	15
8	sunflower	floret formation	3 ^a
9	<i>Euplotes</i> (a ciliate) macronucleus (Ringertz & Hoskins 1965), figure 11	DNA replication	
	<i>Euplotes</i> (a ciliate) macronucleus (Ringertz & Hoskins 1965), figure 11	DNA replication early	1
	<i>Euplotes</i> (a ciliate) macronucleus (Ringertz & Hoskins 1965), figure 11	DNA replication late	8
10	leech embryo axons (Braun & Stent 1989)	elongation rate	4
11	rat embryonic hippocampal axons (Ruthel & Banker 1998), figure 12	growth cone formation	14

^a This figure was obtained by multiplying the formation of 4–5 floret rings per day under optimal conditions (Palmer 1996) by a ring width of 110 μm (Hernandez & Green 1993).

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NOTICE OF CORRECTION

Paragraph 2 §1, the final paragraph of §2, paragraph 3 of §3 and table 1 are now presented in the correct form.
25 January 2008