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Review

### Ion Transport in Sperm Signaling

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### Abstract

Ion channels and transporters, key elements in sperm–egg signaling and environmental sensing, are essential for fertilization. External cues and components from the outer envelopes of the egg influence sperm ion permeability and behavior. Combining *in vivo* measurements of membrane potential, intracellular ions, and second messengers with new molecular approaches and reconstitution strategies are revealing how sperm ion channels participate in motility, sperm maturation, and the acrosome reaction. Sperm are tiny differentiated terminal cells unable to synthesize proteins and difficult to characterize electrophysiologically. Spermatogenic cells, the progenitors of sperm, have become useful tools for probing sperm ion channels since they are larger and molecular biology techniques can be applied. These complementary strategies are opening new avenues to determine how sperm ion channels function in gamete signaling.

### Keywords

acrosome reaction; capacitation; fertilization; ion channels; ion transport; sperm; spermatogenic cells

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### References

#### REFERENCES

- 1 A.P. Alves, B. Mulloy, J.A. Diniz, P.A. Mourao  
**Sulfated polysaccharides from the egg jelly layer are species-specific inducers of acrosomal reaction in sperms of sea urchins**  
J. Biol. Chem., 272 (1997), pp. 6965-6971
- 2 A.P. Alves, B. Mulloy, G.W. Moy, V.D. Vacquier, P.A. Mourao  
**Females of the sea urchin *Strongylocentrotus purpuratus* differ in the structures of their egg jelly sulfated fucans**  
Glycobiology, 8 (1998), pp. 939-946
- 3 M.A. Amaout  
**Molecular genetics and pathogenesis of autosomal dominant polycystic kidney disease**  
Annu. Rev. Med., 52 (2001), pp. 93-123
- 4 C. Arnoult, R.A. Cardullo, J.R. Lemos, H.M. Florman  
**Activation of mouse sperm T-type Ca<sup>2+</sup> channels by adhesion to the egg zona pellucida**

Feedback

- 5 C. Arnoult, Y. Zeng, H.M. Florman  
**ZP3-dependent activation of sperm cation channels regulates acrosomal secretion during mammalian fertilization**  
J. Cell Biol., 134 (1996), pp. 637-645
- 6 C. Arnoult, J.R. Lemos, H.M. Florman  
**Voltage-dependent modulation of T-type calcium channels by protein tyrosine phosphorylation**  
EMBO J., 16 (1997), pp. 1593-1599
- 7 C. Arnoult, M. Villaz, H.M. Florman  
**Pharmacological properties of the T-type  $\text{Ca}^{2+}$  current of mouse spermatogenic cells**  
Mol. Pharmacol., 53 (1998), pp. 1104-1111
- 8 C. Arnoult, I.G. Kazam, P.E. Visconti, G.S. Kopf, M. Villaz, H.M. Florman  
**Control of the low voltage-activated calcium channel of mouse sperm by egg ZP3 and by membrane hyperpolarization during capacitation**  
Proc. Natl. Acad. Sci. USA, 96 (1999), pp. 6757-6762
- 9 D.F. Babcock, M.M. Bosma, D.E. Battaglia, A. Darszon  
**Early persistent activation of sperm  $\text{K}^+$  channels by the egg peptide speract**  
Proc. Natl. Acad. Sci. USA, 89 (1992), pp. 6001-6005
- 10 E. Baldi, M. Luconi, L. Bonaccorsi, M. Muratori, G. Forti  
**Intracellular events and signaling pathways involved in sperm acquisition of fertilizing capacity and acrosome reaction**  
Front. Biosci., 5 (2000), pp. E110-E123
- 11 G.J. Barritt  
**Receptor-activated  $\text{Ca}^{2+}$  inflow in animal cells: A variety of pathways tailored to meet different intracellular  $\text{Ca}^{2+}$  signalling requirements**  
Biochem. J., 337 (1999), pp. 153-169
- 12 C. Beltrán, A. Darszon, P. Labarca, A. Lievano  
**A high-conductance voltage-dependent multistate  $\text{Ca}^{2+}$  channel found in sea urchin and mouse spermatozoa**  
FEBS Lett., 338 (1994), pp. 23-26  
Article  PDF (480KB)
- 13 C. Beltrán, O. Zapata, A. Darszon  
**Membrane potential regulates sea urchin sperm adenylylcyclase**  
Biochemistry, 35 (1996), pp. 7591-7598
- 14 S. Benoff  
**Voltage dependent calcium channels in mammalian spermatozoa**  
Front. Biosci., 3 (1998), pp. D1220-D1240
- 15 J.K. Bentley, A.S. Khatra, D.L. Garbers  
**Receptor-mediated activation of detergent-solubilized guanylate cyclase**  
Biol. Reprod., 39 (1988), pp. 639-647
- 16 P.F. Blackmore  
**Thapsigargin elevates and potentiates the ability of progesterone to increase intracellular free calcium in human sperm: Possible role of perinuclear calcium**  
Cell Calcium, 14 (1993), pp. 53-60  
Article  PDF (777KB)
- 17 P.F. Blackmore, S. Eisoldt  
**The neoglycoprotein mannose-bovine serum albumin, but not progesterone, activates T-type calcium channels in human spermatozoa**  
Mol. Hum. Reprod., 5 (1999), pp. 498-506
- 18 P.F. Blackmore  
**Extragenomic actions of progesterone in human sperm and progesterone metabolites in human platelets**  
Sternschr. 64 (1999) pp. 149-156

- 19 M.R. Bösl, V. Stein, C. Hubner, A.A. Zdebik, S.E. Jordt, A.K. Mukhopadhyay, M.S. Davidoff, A.F. Holstein, T.J. Jentsch  
**Male germ cells and photoreceptors, both dependent on close cell-cell interactions, degenerate upon ClC-2 Cl(-) channel disruption**  
EMBO J., 20 (2001), pp. 1289-1299
- 20 G. Boulay, D.M. Brown, N. Qin, M. Jiang, A. Dietrich, M.X. Zhu, Z. Chen, M. Bimbaumer, K. Mikoshiba, L. Bimbaumer  
**Modulation of Ca<sup>2+</sup> entry by polypeptides of the inositol 1,4,5-trisphosphate receptor (IP3R) that bind transient receptor potential (TRP): Evidence for roles of TRP and IP3R in store depletion-activated Ca<sup>2+</sup> entry**  
Proc. Natl. Acad. Sci. USA, 96 (1999), pp. 14955-14960
- 21 H. Breitbart, Z. Naor  
**Protein kinases in mammalian sperm capacitation and the acrosome reaction**  
Rev. Reprod., 4 (1999), pp. 151-159
- 22 J.H.B. Bridge  
N. Sperelakis (Ed.), Cell Physiology Sourcebook: A Molecular Approach, Academic Press, San Diego (2001), pp. 283-300
- 23 C.J. Brokaw  
**Calcium-induced asymmetrical beating of triton-demembranated sea urchin sperm flagella**  
J. Cell Biol., 82 (1979), pp. 401-411
- 24 M. Bycroft, A. Bateman, J. Clarke, S.J. Hamill, R. Sandford, R.L. Thomas, C. Chothia  
**The structure of a PKD domain from polycystin-1: Implications for polycystic kidney disease**  
EMBO J., 18 (1999), pp. 297-305
- 25 H.C. Chan, W.L. Wu, Y.P. Sun, P.S. Leung, T.P. Wong, Y.W. Chung, S.C. So, T.S. Zhou, Y.C. Yan  
**Expression of sperm Ca<sup>2+</sup>-activated K<sup>+</sup> channels in Xenopus oocytes and their modulation by extracellular ATP**  
FEBS Lett., 438 (1998), pp. 177-182  
Article  PDF (114KB)
- 26 Y. Chen, M.J. Cann, T.N. Litvin, V. Iourgenko, M.L. Sinclair, L.R. Levin, J. Buck  
**Soluble adenylyl cyclase as an evolutionarily conserved bicarbonate sensor**  
Science, 289 (2000), pp. 625-628
- 27 D.L. Clapper, J.A. Davis, P.J. Lamothe, C. Patton, D. Epel  
**Involvement of zinc in the regulation of pH<sub>i</sub>, motility, and acrosome reactions in sea urchin sperm**  
J. Cell Biol., 100 (1985), pp. 1817-1824
- 28 S.P. Cook, D.F. Babcock  
**Activation of Ca<sup>2+</sup> permeability by cAMP is coordinated through the pH<sub>i</sub> increase induced by speract**  
J. Biol. Chem., 268 (1993), pp. 22408-22413
- 29 S.P. Cook, C.J. Brokaw, C.H. Muller, D.F. Babcock  
**Sperm chemotaxis: Egg peptides control cytosolic calcium to regulate flagellar responses**  
Dev. Biol., 165 (1994), pp. 10-19  
Article  PDF (620KB)
- 30 J.C. Dan  
**Studies on the acrosome. III. Effect of calcium deficiency**  
Biol. Bull., 107 (1954), pp. 335-349
- 31 L.J. Dangott, D.L. Garbers  
**Identification and partial characterization of the receptor for speract**  
J. Biol. Chem., 259 (1984), pp. 13712-13716
- 32 A. Darszon, P. Labarca, T. Nishigaki, F. Espinosa  
**Ion channels in sperm physiology**  
Physiol. Rev., 79 (1999), pp. 481-510
- 33 S.E. Domino, S.B. Bocckino, D.L. Garbers  
**Activation of phospholipase D by the fucose-sulfate glycoconjugate that induces an acrosome reaction in spermatozoa**

- 34 E. Dragileva, S. Rubinstein, H. Breitbart  
**Intracellular Ca<sup>2+</sup>-Mg<sup>2+</sup>-ATPase regulates calcium influx and acrosomal exocytosis in bull and ram spermatozoa**  
Biol. Reprod., 61 (1999), pp. 1226-1234
- 35 M. Eisenbach  
**Mammalian sperm chemotaxis and its association with capacitation**  
Dev. Genet., 25 (1999), pp. 87-94
- 36 Y. Endo, M.A. Lee, G.S. Kopf  
**Characterization of an islet-activating protein-sensitive site in mouse sperm that is involved in the zona pellucida-induced acrosome reaction**  
Dev. Biol., 129 (1988), pp. 12-24  
Article  PDF (4MB)
- 37 F. Espinosa, J.L. De la Vega-Beltrán, I. López-González, R. Delgado, P. Labarca, A. Darszon  
**Mouse sperm patch-clamp recording reveal single Cl<sup>-</sup> channels sensitive to niflumic acid, a blocker of the sperm acrosome reaction**  
FEBS Lett., 426 (1998), pp. 47-51  
Article  PDF (261KB)
- 38 F. Espinosa, I. López-González, C.J. Serrano, G. Gasque, J.L. de la Vega-Beltrán, C.L. Treviño, A. Darszon  
**Anion channel blockers differentially affect T-type Ca<sup>2+</sup> currents of mouse spermatogenic cells, alpha1E currents expressed in Xenopus oocytes and the sperm acrosome reaction**  
Dev. Genet., 25 (1999), pp. 103-114
- 39 F. Espinosa, I. López-González, C. Muñoz-Garay, R. Felix, J.L. de la Vega-Beltrán, G.S. Kopf, P.E. Visconti, A. Darszon  
**Dual regulation of the T-type Ca<sup>2+</sup> current by serum albumin and beta-estradiol in mammalian spermatogenic cells**  
FEBS Lett., 475 (2000), pp. 251-256  
Article  PDF (255KB)
- 40 H.A.J. Farach, D.I. Mundy, W.J. Strittmatter, W.J. Lennarz  
**Evidence for the involvement of metalloendoproteases in the acrosome reaction in sea urchin sperm**  
J. Biol. Chem., 262 (1987), pp. 5483-5487
- 41 F.M. Flesch, B.M. Gadella  
**Dynamics of the mammalian sperm plasma membrane in the process of fertilization**  
Biochim. Biophys. Acta, 1469 (2000), pp. 197-235  
Article  PDF (1MB)
- 42 H.M. Florman, R.M. Tombes, N.L. First, D.F. Babcock  
**An adhesion-associated agonist from the zona pellucida activates G protein-promoted elevations of internal Ca<sup>2+</sup> and pH that mediate mammalian sperm acrosomal exocytosis**  
Dev. Biol., 135 (1989), pp. 133-146  
Article  PDF (5MB)
- 43 H.M. Florman, M.E. Corron, T.D. Kim, D.F. Babcock  
**Activation of voltage-dependent calcium channels of mammalian sperm is required for zona pellucida-induced acrosomal exocytosis**  
Dev. Biol., 152 (1992), pp. 304-314  
Article  PDF (1MB)
- 44 H.M. Florman  
**Sequential focal and global elevations of sperm intracellular Ca<sup>2+</sup> are initiated by the zona pellucida during acrosomal exocytosis**  
Dev. Biol., 165 (1994), pp. 152-164  
Article  PDF (842KB)
- 45 H.M. Florman, C. Arnoult, I.G. Kazam, C. Li, C.M. O'Toole  
**A perspective on the control of mammalian fertilization by egg-activated ion channels in sperm: A tale of two channels**  
Biol. Reprod., 59 (1998), pp. 12-16

- 46 C. Foresta, M. Rossato, F. Di Virgilio  
**Ion fluxes through the progesterone-activated channel of the sperm plasma membrane**  
Biochem. J., 294 (1993), pp. 279-283
- 47 L.R. Fraser  
**Cellular biology of capacitation and the acrosome reaction**  
Hum. Reprod., 10 (1995), pp. 22-30
- 48 K. Fukami, K. Nakao, T. Inoue, Y. Kataoka, M. Kurokawa, R.A. Fissore, K. Nakamura, M. Katsuki, K. Mikoshiba, N. Yoshida, T. Takenawa  
**Requirement of phospholipase C $\delta$ 4 for the zona pellucida-induced acrosome reaction**  
Science, 292 (2001), pp. 920-923
- 49 B.E. Galindo, C. Beltrán, E.J.J. Cragoe, A. Darszon  
**Participation of a K<sup>+</sup> channel modulated directly by cGMP in the speract-induced signaling cascade of strongylocentrotus purpuratus sea urchin sperm**  
Dev. Biol., 221 (2000), pp. 285-294  
Article  PDF (202KB)
- 50 Z Gao, D.L. Garbers  
**Species diversity in the structure of zonadhesin, a sperm-specific membrane protein containing multiple cell adhesion molecule-like domains**  
J. Biol. Chem., 273 (1998), pp. 3415-3421
- 51 D.L. Garbers  
**Molecular basis of fertilization**  
Annu. Rev. Biochem., 58 (1989), pp. 719-742
- 52 M.A. Garcia, S. Meizel  
**Regulation of intracellular pH in capacitated human spermatozoa by a Na<sup>+</sup>/H<sup>+</sup> exchanger**  
Mol. Reprod. Dev., 52 (1999), pp. 189-195
- 53 J. García-Soto, M. González-Martínez, L. de De La Torre, A. Darszon  
**Internal pH can regulate Ca<sup>2+</sup> uptake and the acrosome reaction in sea urchin sperm**  
Dev. Biol., 120 (1987), pp. 112-120  
Article  PDF (1MB)
- 54 R. Gauss, R. Seifert, U.B. Kaupp  
**Molecular identification of a hyperpolarization-activated channel in sea urchin sperm**  
Nature, 393 (1998), pp. 583-587
- 55 M. González-Martínez, A. Darszon  
**A fast transient hyperpolarization occurs during the sea urchin sperm acrosome reaction induced by egg jelly**  
FEBS Lett., 218 (1987), pp. 247-250  
Article  PDF (358KB)
- 56 M.T. González-Martínez, A. Guerrero, E. Morales, L. de De La Torre, A. Darszon  
**A depolarization can trigger Ca<sup>2+</sup> uptake and the acrosome reaction when preceded by a hyperpolarization in *L. pictus* sea urchin sperm**  
Dev. Biol., 150 (1992), pp. 193-202  
Article  PDF (1MB)
- 57 M. González-Martínez, B.E. Galindo, L. de De La Torre, O. Zapata, E. Rodríguez, H.M. Florman, A. Darszon  
**A sustained increase in intracellular Ca<sup>2+</sup> is required for the acrosome reaction in sea urchin sperm**  
Dev. Biol., 235 (2001)
- 58 S. Gonzalez-Perret, K. Kim, C. Ibarra, A.E. Damiano, E. Zotta, M. Batelli, P.C. Harris, I.L. Reisin, M.A. Amaout, H.F. Cantiello  
**Polycystin-2, the protein mutated in autosomal dominant polycystic kidney disease (ADPKD), is a Ca<sup>2+</sup>-permeable nonselective cation channel**  
Proc. Natl. Acad. Sci. USA, 98 (2001), pp. 1182-1187
- 59 L.O. Goodwin, N.B. Leeds, I. Hurley, F.S. Mandel, R.G. Pergolizzi, S. Benoff  
**Isolation and characterization of the primary structure of testis-specific L-type calcium channel: Implications for contraception**  
Mol. Hum. Reprod., 2 (1997), pp. 255-260

- 60 A. Guerrero, A. Darszon  
**Egg jelly triggers a calcium influx which inactivates and is inhibited by calmodulin antagonists in the sea urchin sperm**  
Biochim. Biophys. Acta, 980 (1989), pp. 109-116  
Article  PDF (614KB)
- 61 A. Guerrero, A. Darszon  
**Evidence for the activation of two different  $\text{Ca}^{2+}$  channels during the egg jelly-induced acrosome reaction of sea urchin sperm**  
J. Biol. Chem., 264 (1989), pp. 19593-19599
- 62 A. Guerrero, L. Garcia, O. Zapata, E. Rodriguez, A. Darszon  
**Acrosome reaction inactivation in sea urchin sperm**  
Biochim. Biophys. Acta, 1401 (1998), pp. 329-338  
Article  PDF (235KB)
- 63 S. Hagiwara, K. Kawa  
**Calcium and potassium currents in spermatogenic cells dissociated from rat seminiferous tubules**  
J. Physiol., 356 (1984), pp. 135-149
- 64 K. Hanaoka, F. Qian, A. Boletta, A.K. Bhunia, K. Piontek, L. Tsiokas, V.P. Sukhatme, W.B. Guggino, G.G. Germino  
**Co-assembly of polycystin-1 and -2 produces unique cation-permeable currents**  
Nature, 408 (2000), pp. 990-994
- 65 T. Harumi, K. Hoshino, N. Suzuki  
**Effects of sperm-activating peptide I on *Hemicentrotus pulcherrimus* spermatozoa in high potassium sea water**  
Dev. Growth Differ., 34 (1992), pp. 163-172
- 66 E. Herrera, K. Salas, N. Lagos, D.J. Benos, J.G. Reyes  
**Energy metabolism and its linkage to intracellular  $\text{Ca}^{2+}$  and pH regulation in rat spermatogenic cells**  
Biol. Cell, 92 (2000), pp. 429-440  
Article  PDF (1MB)
- 67 Bertil Hille  
Ion Channels of Excitable Membranes, Sinauer, Sunderland (1992)
- 68 M. Hoshi, T. Nishigaki, A. Ushiyama, T. Okinaga, K. Chiba, M. Matsumoto  
**Egg-jelly signal molecules for triggering the acrosome reaction in starfish spermatozoa**  
Int. J. Dev. Biol., 38 (1994), pp. 167-174
- 69 J. Hughes, C.J. Ward, R. Aspinwall, R. Butler, P.C. Harris  
**Identification of a human homologue of the sea urchin receptor for egg jelly: A polycystic kidney disease-like protein**  
Hum. Mol. Genet., 8 (1999), pp. 543-549
- 70 H. Izumi, T. Marian, K. Inaba, Y. Oka, M. Morisawa  
**Membrane hyperpolarization by sperm-activating and -attracting factor increases cAMP level and activates sperm motility in the ascidian *Ciona intestinalis***  
Dev. Biol., 213 (1999), pp. 246-256  
Article  PDF (153KB)
- 71 A. Jacob, I.R. Hurley, L.O. Goodwin, G.W. Cooper, S. Benoff  
**Molecular characterization of a voltage-gated potassium channel expressed in rat testis**  
Mol. Hum. Reprod., 6 (2000), pp. 303-313
- 72 L.Y. Jan, Y.N. Jan  
**Cloned potassium channels from eukaryotes and prokaryotes**  
Annu. Rev. Neurosci., 20 (1997), pp. 91-123
- 73 M.K. Jungnickel, H. Marrero, L. Birnbaumer, J.R. Lemos, H.M. Florman  
**Trp2 regulates entry of  $\text{Ca}^{2+}$  into mouse sperm triggered by egg ZP3**  
Nat. Cell. Biol., 3 (2001), pp. 499-502
- 74 K. Katafuchi, T. Mori, K. Toshimori, H. Iida  
**Localization of a syntaxin isoform, syntaxin 2, to the acrosomal region of rodent spermatozoa**

- 75 U.B. Kaupp  
**Family of cyclic nucleotide gated ion channels**  
Curr. Opin. Neurobiol., 5 (1995), pp. 434-442  
Article  PDF (869KB)
- 76 U. Kaupp, R. Seifert  
**Molecular diversity of pacemaker ion channels**  
Annu. Rev. Physiol., 63 (2001), pp. 235-257
- 77 A.L. Kierszenbaum  
**Fusion of membranes during the acrosome reaction: A tale of two SNAREs**  
Mol. Reprod. Dev., 57 (2000), pp. 309-310
- 78 J.C. Kirkman-Brown, C. Bray, P.M. Stewart, C.L. Barratt, S.J. Publicover  
**Biphasic elevation of  $[Ca^{2+}]_i$  in individual human spermatozoa exposed to progesterone**  
Dev. Biol., 222 (2000), pp. 326-335  
Article  PDF (278KB)
- 79 S. Koyota, K.M. Wimalasiri, M. Hoshi  
**Structure of the main saccharide chain in the acrosome reaction-inducing substance of the starfish, Asterias amurensis**  
J. Biol. Chem., 272 (1997), pp. 10372-10376
- 80 Z Krasznai, T. Marian, H. Izumi, S. Damjanovich, L. Balkay, L. Tron, M. Morisawa  
**Membrane hyperpolarization removes inactivation of  $Ca^{2+}$  channels, leading to  $Ca^{2+}$  influx and subsequent initiation of sperm motility in the common carp**  
Proc. Natl. Acad. Sci. USA, 97 (2000), pp. 2052-2057
- 81 R.C. Kuo, G.T. Baxter, S.H. Thompson, S.A. Stricker, C. Patton, J. Bonaventura, D. Epel  
**NO is necessary and sufficient for egg activation at fertilization**  
Nature, 406 (2000), pp. 633-636
- 82 P. Labarca, C. Santi, O. Zapata, E. Morales, C. Beltrán, A. Liévano, A. Darszon  
**A cAMP regulated  $K^+$ -selective channel from the sea urchin sperm plasma membrane**  
Dev. Biol., 174 (1996), pp. 271-280  
Article  PDF (162KB)
- 83 H.C. Lee, D.L. Garbers  
**Modulation of the voltage-sensitive  $Na^+/H^+$  exchange in sea urchin spermatozoa through membrane potential changes induced by the egg peptide speract**  
J. Biol. Chem., 261 (1986), pp. 16026-16032
- 84 A. Lievano, J.A. Sanchez, A. Darszon  
**Single-channel activity of bilayers derived from sea urchin sperm plasma membranes at the tip of a patch-clamp electrode**  
Dev. Biol., 112 (1985), pp. 253-257  
Article  PDF (499KB)
- 85 A. Lievano, E.C. Vega-SaenzdeMiera, A. Darszon  
 **$Ca^{2+}$  channels from the sea urchin sperm plasma membrane**  
J. Gen. Physiol., 95 (1990), pp. 273-296
- 86 A. Lievano, C.M. Santi, C.J. Serrano, C.L. Trevino, A.R. Bellve, A. Hernandez-Cruz, A. Darszon  
**T-type  $Ca^{2+}$  channels and alpha1E expression in spermatogenic cells, and their possible relevance to the sperm acrosome reaction**  
FEBS Lett., 388 (1996), pp. 150-154  
Article  PDF (529KB)
- 87 F.R. Lillie  
Problems of Fertilization, University of Chicago Press, Chicago (1919)
- 88 M.N. Llanos, A.M. Ronco, M.C. Aguirre, S. Meizel  
**Hamster sperm glycine receptor: Evidence for its presence and involvement in the acrosome reaction**

- 89 S. Maddocks, B.P. Setchell  
**The physiology of the endocrine testis**  
Oxford Rev. Reprod. Biol., 10 (1988), pp. 53-123
- 90 S.B. McLeskey, C. Dowds, R. Carballada, R.R. White, P.M. Saling  
**Molecules involved in mammalian sperm-egg interaction**  
Int. Rev. Cytol., 177 (1998), pp. 57-113
- 91 S. Meizel, K.O. Turner  
**Initiation of the human sperm acrosome reaction by thapsigargin**  
J. Exp. Zool., 267 (1993), pp. 350-355
- 92 S. Meizel, K.O. Turner, R. Nuccitelli  
**Progesterone triggers a wave of increased free calcium during the human sperm acrosome reaction**  
Dev. Biol., 182 (1997), pp. 67-75  
Article  PDF (372KB)
- 93 S. Meizel  
**Amino acid neurotransmitter receptor/chloride channels of mammalian sperm and the acrosome reaction**  
Biol. Reprod., 56 (1997), pp. 569-574
- 94 C.S. Melendrez, S. Meizel  
**Studies of porcine and human sperm suggesting a role for a sperm glycine receptor/Cl<sup>-</sup> channel in the zona pellucida-initiated acrosome reaction**  
Biol. Reprod., 53 (1995), pp. 676-683
- 95 K.J. Mengerink, G.W. Moy, V.D. Vacquier  
**suREJ proteins: New signalling molecules in sea urchin spermatozoa**  
Zygote, 8 (2000), pp. S28-S30
- 96 M. Michaut, C.N. Tomes, G. De Blas, R. Yunes, L.S. Mayorga  
**Calcium-triggered acrosomal exocytosis in human spermatozoa requires the coordinated activation of Rab3A and N-ethylmaleimide-sensitive factor**  
Proc. Natl. Acad. Sci. USA, 97 (2000), pp. 9996-10001
- 97 R.L. Miller  
C.B. Metz, A. Monroy (Eds.), Biology of Fertilization, Academic Press, New York (1985), pp. 275-337  
Article  PDF (5MB)
- 98 R.L. Miller, R. Vogt  
**An N-terminal partial sequence of the 13 kDa Pycnopodia helianthoides sperm chemoattractant "startrak" possesses sperm-attracting activity**  
J. Exp. Biol., 199 (1996), pp. 311-318
- 99 E. Morales, L. de la Torre, G.W. Moy, V.D. Vacquier, A. Darszon  
**Anion channels in the sea urchin sperm plasma membrane**  
Mol. Reprod. Dev., 36 (1993), pp. 174-182
- 100 M. Morisawa  
**Cell signaling mechanisms for sperm motility**  
Zool. Sci., 11 (1994), pp. 647-662
- 101 G.W. Moy, L.M. Mendoza, J.R. Schulz, W.J. Swanson, C.G. Glabe, V.D. Vacquier  
**The sea urchin sperm receptor for egg jelly is a modular protein with extensive homology to the human polycystic kidney disease protein, PKD1**  
J. Cell Biol., 133 (1996), pp. 809-817
- 102 C. Munoz-Garay, J.L. de la Vega-Beltran, R. Delgado, P. Labarca, R. Felix, A. Darszon  
**Inwardly rectifying K(+) channels in spermatogenic cells: Functional expression and implication in sperm capacitation**  
Dev. Biol., 234 (2001), pp. 261-274  
Article  PDF (290KB)

- 103 T. Murase, E.R. Roldan  
**Progesterone and the zona pellucida activate different transducing pathways in the sequence of events leading to diacylglycerol generation during mouse sperm acrosomal exocytosis**  
Biochem. J., 320 (1996), pp. 1017-1023
- 104 T. Nishigaki, K. Chiba, W. Miki, M. Hoshi  
**Structure and function of asterosaps, sperm-activating peptides from the jelly coat of starfish eggs**  
Zygote, 4 (1996), pp. 237-245
- 105 T. Nishigaki, A. Darszon  
**Real-time measurements of the interactions between fluorescent speract and its sperm receptor**  
Dev. Biol., 223 (2000), pp. 17-26  
Article  PDF (147KB)
- 106 T. Nishigaki, F.Z. Zamudio, L.D. Possani, A. Darszon  
**Time-resolved sperm responses to an egg peptide measured by stopped-flow fluorometry**  
Biochem. Biophys. Res. Commun., 284 (2001), pp. 531-535  
Article  PDF (141KB)
- 107 H. Nomura, A.E. Turco, Y. Pei, L. Kalaydjieva, T. Schiavello, S. Weremowicz, W. Ji, C.C. Morton, M. Meisler, S.T. Reeders, J. Zhou  
**Identification of PKDL, a novel polycystic kidney disease 2-like gene whose murine homologue is deleted in mice with kidney and retinal defects**  
J. Biol. Chem., 273 (1998), pp. 25967-25973
- 108 S. Oda, Y. Igarashi, K. Manaka, N. Koibuchi, M. Sakai-Sawada, K. Sakai, M. Morisawa, H. Ohtake, N. Shimizu  
**Sperm-activating proteins obtained from the herring eggs are homologous to trypsin inhibitors and synthesized in follicle cells**  
Dev. Biol., 204 (1998), pp. 55-63  
Article  PDF (538KB)
- 109 K. Ohta, C. Sato, T. Matsuda, M. Toriyama, V.D. Vacquier, W.J. Lennarz, K. Kitajima  
**Co-localization of receptor and transducer proteins in the glycosphingolipid-enriched, low density, detergent-insoluble membrane fraction of sea urchin sperm**  
Glycoconj. J., 17 (2000), pp. 205-214
- 110 N. Okamura, Y. Tajima, A. Soejima, H. Masuda, Y. Sugita  
**Sodium bicarbonate in seminal plasma stimulates the motility of mammalian spermatozoa through direct activation of adenylate cyclase**  
J. Biol. Chem., 260 (1985), pp. 9699-9705
- 111 C.M. O'Toole, C. Arnoult, A. Darszon, R.A. Steinhardt, H.M. Florman  
**Ca<sup>2+</sup> entry through store-operated channels in mouse sperm is initiated by egg ZP3 and drives the acrosome reaction**  
Mol. Biol. Cell, 11 (2000), pp. 1571-1584
- 112 A.B. Parekh, R. Penner  
**Store depletion and calcium influx**  
Physiol. Rev., 77 (1997), pp. 901-930
- 113 C. Patrat, J.P. Wolf, S. Epelboin, J.N. Hugues, F. Olivennes, P. Granet, J.R. Zorn, P. Jouannet  
**Pregnancies, growth and development of children conceived by subzonal injection of spermatozoa**  
Hum. Reprod., 14 (1999), pp. 2404-2410
- 114 S.J. Publicover, C.L. Barratt  
**Voltage-operated Ca<sup>2+</sup> channels and the acrosome reaction: Which channels are present and what do they do?**  
Hum. Reprod., 14 (1999), pp. 873-879
- 115 J.W.J. Putney, R.R. McKay  
**Capacitative calcium entry channels**  
BioEssays, 21 (1999), pp. 38-46
- 116 J. Ramalho-Santos, R.D. Moreno, P. Sutovsky, A.W. Chan, L. Hewitson, G.M. Wessel, C.R. Simerly, G. Schatten  
**SNAREs in mammalian sperm: Possible implications for fertilization**  
Dev. Biol., 223 (2000), pp. 54-69

- 117 E. Reynaud, T. De de La, O. Zapata, A. Lievano, A. Darszon  
**Ionic bases of the membrane potential and intracellular pH changes induced by speract in swollen sea urchin sperm**  
FEBS Lett., 329 (1993), pp. 210-214  
Article  PDF (589KB)
- 118 S.G. Rhee, Y.S. Bae  
**Regulation of phosphoinositide-specific phospholipase C isozymes**  
J. Biol. Chem., 272 (1997), pp. 15045-15048
- 119 E.R. Roldan, T. Murase, Q.X. Shi  
**Exocytosis in spermatozoa in response to progesterone and zona pellucida**  
Science, 266 (1994), pp. 1578-1581
- 120 E.R. Roldan  
**Role of phospholipases during sperm acrosomal exocytosis**  
Front. Biosci., 3 (1998), pp. D1109-D1119
- 121 L. Salvatore, M.C. D'Adamo, R. Polishchuk, M. Salmona, M. Pessia  
**Localization and age-dependent expression of the inward rectifier K<sup>+</sup> channel subunit Kir 5.1 in a mammalian reproductive system**  
FEBS Lett., 449 (1999), pp. 146-152  
Article  PDF (1MB)
- 122 D. Sánchez, P. Labarca, A. Darszon  
**Sea urchin sperm cation-selective channels directly modulated by cAMP**  
FEBS Lett., 503 (2001), pp. 111-115  
Article  PDF (177KB)
- 123 C.M. Santi, A. Darszon, A. Hernandez-Cruz  
**A dihydropyridine-sensitive T-type Ca<sup>2+</sup> current is the main Ca<sup>2+</sup> current carrier in mouse primary spermatocytes**  
Am. J. Physiol., 271 (1996), pp. C1583-C1593
- 124 C.M. Santi, T. Santos, A. Hernandez-Cruz, A. Darszon  
**Properties of a novel pH-dependent Ca<sup>2+</sup> permeation pathway present in male germ cells with possible roles in spermatogenesis and mature sperm function**  
J. Gen. Physiol., 112 (1998), pp. 33-53
- 125 Y. Sato, J.H. Son, R.P. Tucker, S. Meizel  
**The zona pellucida-initiated acrosome reaction: Defect due to mutations in the sperm glycine receptor/Cl(-) channel**  
Dev. Biol., 227 (2000), pp. 211-218  
Article  PDF (151KB)
- 126 R.W. Schackmann, P.B. Chock  
**Alteration of intracellular Ca<sup>2+</sup> in sea urchin sperm by the egg peptide speract. Evidence that increased intracellular Ca<sup>2+</sup> is coupled to Na<sup>+</sup> entry and increased intracellular pH**  
J. Biol. Chem., 261 (1986), pp. 8719-8728
- 127 R.W. Schackmann  
H. Schatte, G. Schatten (Eds.), The Cell Biology of Fertilization, Academic Press, San Diego (1989), pp. 3-28  
Article  PDF (1MB)
- 128 M. Schreiber, A. Wei, A. Yuan, J. Gaut, M. Saito, L. Salkoff  
**Slo3, a novel pH-sensitive K<sup>+</sup> channel from mammalian spermatocytes**  
J. Biol. Chem., 273 (1998), pp. 3509-3516
- 129 J.R. Schulz, J.D. Sasaki, V.D. Vacquier  
**Increased association of synapsosome-associated protein of 25 kDa with syntaxin and vesicle-associated membrane protein following acrosomal exocytosis of sea urchin sperm**  
J. Biol. Chem., 273 (1998), pp. 24355-24359
- 130 C.J. Serrano, C.L. Trevino, R. Felix, A. Darszon

- 131 X Shi, S. Amindari, K. Paruchuru, D. Skalla, H. Burkin, B.D. Shur, D.J. Miller  
**Cell surface beta-1,4-galactosyltransferase-I activates G protein-dependent exocytotic signaling**  
Development, 128 (2001), pp. 645-654
- 132 M.L. Sinclair, X.Y. Wang, M. Mattia, M. Conti, J. Buck, D.J. Wolgemuth, L.R. Levin  
**Specific expression of soluble adenyl cyclase in male germ cells**  
Mol. Reprod. Dev., 56 (2000), pp. 6-11
- 133 S. Singh, D.G. Lowe, D.S. Thorpe, H. Rodriguez, W.J. Kuang, L.J. Dangott, M. Chinkers, D.V. Goeddel, D.L. Garbers  
**Membrane guanylate cyclase is a cell-surface receptor with homology to protein kinases**  
Nature, 334 (1988), pp. 708-712
- 134 A.B. Smith  
**Phylogenetic relationship, divergence times and rates of molecular evolution for camarodont sea urchins**  
Mol. Biol. Evol., 5 (1988), pp. 345-365
- 135 S.S. Suarez  
**Hyperactivated motility in sperm**  
J. Androl., 17 (1996), pp. 331-335
- 136 N. Suzuki  
**Structure, function and biosynthesis of sperm-activating peptides and fucose sulfate glycoconjugate in the extracellular coat of sea urchin eggs**  
Zool. Sci., 12 (1995), pp. 13-27
- 137 C.N. Tomes, C.R. McMaster, P.M. Saling  
**Activation of mouse sperm phosphatidylinositol-4,5 bisphosphate-phospholipase C by zona pellucida is modulated by tyrosine phosphorylation**  
Mol. Reprod. Dev., 43 (1996), pp. 196-204
- 138 C.L. Treviño, C.M. Santi, C. Beltrán, A. Hernández-Cruz, A. Darszon, H. Lomeli  
**Localisation of inositol trisphosphate and ryanodine receptors during mouse spermatogenesis: Possible functional implications**  
Zygote, 6 (1998), pp. 159-172
- 139 V.D. Vacquier  
**Evolution of gamete recognition proteins**  
Science, 281 (1998), pp. 1995-1998
- 140 V.D. Vacquier, G.W. Moy  
**The fucose sulfate polymer of egg jelly binds to sperm REJ and is the inducer of the sea urchin sperm acrosome reaction**  
Dev. Biol., 192 (1997), pp. 125-135  
Article  PDF (378KB)
- 141 T. Vanha-Perttula, J. Kasurinen  
**Purification and characterization of phosphatidylinositol-specific phospholipase C from bovine spermatozoa**  
Int. J. Biochem., 21 (1989), pp. 997-1007  
Article  PDF (1MB)
- 142 B. Vannier, M. Peyton, G. Boulay, D. Brown, N. Qin, M. Jiang, X. Zhu, L. Birnbaumer  
**Mouse trp2, the homologue of the human trpc2 pseudogene, encodes mTrp2, a store depletion-activated capacitative Ca<sup>2+</sup> entry channel**  
Proc. Natl. Acad. Sci. USA, 96 (1999), pp. 2060-2064
- 143 P.E. Visconti, J.G. Tezon  
**Phorbol esters stimulate cyclic adenosine 3', 5'-monophosphate accumulation in hamster spermatozoa during in vitro capacitation**  
Biol. Reprod., 40 (1989), pp. 223-231
- 144 P.E. Visconti, G.D. Moore, J.L. Bailey, P. Leclerc, S.A. Connors, D. Pan, P. Olds-Clarke, G.S. Kopf  
Contribution of membrane phosphoinositides to protein kinase C activation and capacitation and its regulation by AMP deaminase

**Capacitation of mouse spermatozoa. II. Protein tyrosine phosphorylation and capacitation are regulated by a CAV1-dependent pathway**

Development, 121 (1995), pp. 1139-1150

- 145 P.E. Visconti, H. Galantino-Homer, X. Ning, G.D. Moore, J.P. Valenzuela, C.J. Jorgez, J.G. Alvarez, G.S. Kopf  
**Cholesterol efflux-mediated signal transduction in mammalian sperm. beta-cyclodextrins initiate transmembrane signaling leading to an increase in protein tyrosine phosphorylation and capacitation**  
J. Biol. Chem., 274 (1999), pp. 3235-3242
- 146 W.L. Vredenburgh-Wilberg, J.J. Parrish  
**Intracellular pH of bovine sperm increases during capacitation**  
Mol. Reprod. Dev., 40 (1995), pp. 490-502
- 147 L.D. Walensky, S.H. Snyder  
**Inositol 1,4,5-trisphosphate receptors selectively localized to the acrosomes of mammalian sperm**  
J. Cell Biol., 130 (1995), pp. 857-869
- 148 G.E. Ward, C.J. Brokaw, D.L. Garbers, V.D. Vacquier  
**Chemotaxis of *Arbacia punctulata* spermatozoa to resact, a peptide from the egg jelly layer**  
J. Cell Biol., 101 (1985), pp. 2324-2329
- 149 P.M. Wassarman, L. Jovine, E.S. Litscher  
**A profile of fertilization in mammals**  
Nat. Cell Biol., 3 (2001), pp. E59-E64
- 150 G. Wennemuth, R.E. Westenbroek, T. Xu, B. Hille, D.F. Babcock  
**CaV2.2 and CaV2.3 (N- and R-type) Ca<sup>2+</sup> channels in depolarization-evoked entry of Ca<sup>2+</sup> into mouse sperm**  
J. Biol. Chem., 275 (2000), pp. 21210-21217
- 151 R.E. Westenbroek, D.F. Babcock  
**Discrete regional distributions suggest diverse functional roles of calcium channel alpha1 subunits in sperm**  
Dev. Biol., 207 (1999), pp. 457-469  
Article  PDF (490KB)
- 152 I. Weyand, M. Godde, S. Frings, J. Weiner, F. Muller, W. Altenhofen, H. Hatt, U.B. Kaupp  
**Cloning and functional expression of a cyclic-nucleotide-gated channel from mammalian sperm**  
Nature, 368 (1994), pp. 859-863
- 153 D.R. White, R.J. Aitken  
**Relationship between calcium, cyclic AMP, ATP, and intracellular pH and the capacity of hamster spermatozoa to express hyperactivated motility**  
Gamete Res., 22 (1989), pp. 163-177
- 154 B. Wiesner, J. Weiner, R. Middendorff, V. Hagen, U.B. Kaupp, I. Weyand  
**Cyclic nucleotide-gated channels on the flagellum control Ca<sup>2+</sup> entry into sperm**  
J. Cell Biol., 142 (1998), pp. 473-484
- 155 G. Wu, T. Hayashi, J.H. Park, M. Dixit, D.M. Reynolds, L. Li, Y. Maeda, Y. Cai, M. Coca-Prados, S. Somlo  
**Identification of PKD2L, a human PKD2-related gene: Tissue-specific expression and mapping to chromosome 10q25**  
Genomics, 54 (1998), pp. 564-568  
Article  PDF (287KB)
- 156 R. Yanagimachi  
E. Knobil, J.D. Neill (Eds.), The Physiology of Reproduction, Raven Press, New York (1994), pp. 189-317
- 157 R. Yanagimachi  
**Intracytoplasmic sperm injection experiments using the mouse as a model**  
Hum. Reprod., 13 (1998), pp. 87-98
- 158 K. Yoshino, N. Suzuki  
**Two classes of receptor specific for sperm-activating peptide III in sand-dollar spermatozoa**  
Eur. J. Biochem., 206 (1992), pp. 887-893
- 159 O. Zapata, J. Ralston, C. Beltrán, J.B. Parys, J.L. Chen, F.J. Longo, A. Darszon

- 160 Y. Zeng, E.N. Clark, H.M. Florman

**Sperm membrane potential: Hyperpolarization during capacitation regulates zona pellucida-dependent acrosomal secretion**

Dev. Biol., 171 (1995), pp. 554-563

Article  PDF (600KB)

- 161 Y. Zeng, J.A. Oberdorf, H.M. Florman

**pH regulation in mouse sperm: Identification of  $\text{Na}^+$ -,  $\text{Cl}^-$ , and  $\text{HCO}_3^-$ -dependent and arylaminobenzoate-dependent regulatory mechanisms and characterization of their roles in sperm capacitation**

Dev. Biol., 173 (1996), pp. 510-520

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