Reproductive BioMedicine Online (2011) **23**, 281–289

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SYMPOSIUM: OOCYTE CRYOPRESERVATION
REVIEW

History of oocyte cryopreservation

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Abstract The potential advantages of being able to cryopreserve oocytes have been apparent for many decades. Technical difficulties associated with the unique properties of the mammalian oocyte initially retarded rapid development in this area but recent advances have overcome many of the problems. A stage has now been reached where oocyte cryopreservation can be considered an important component of human assisted reproductive technology.

KEYWORDS: cryopreservation, history, human, oocyte, slow cooling, vitrification

Introduction

The paradoxical effects of low temperature in nature have been known for centuries through examples such as hibernation and frostbite (Boyle, 1683). The ability to achieve preservation of living cells at subzero temperatures was demonstrated in more recent times but continued to elude those with the aim of cryopreserving human oocytes for a significantly longer time. Only now has the potential for successful human oocyte cryopreservation to challenge both practice in assisted reproduction treatment and social attitudes to deferred reproduction become a realistic possibility.

Early days of cryobiology

Although attempts to preserve cells at subzero temperatures had proven almost impossible during the early 1900s, the beneficial effect of dehydration prior to freezing using sugars had been identified (Luyet and Hodapp, 1938). A turning point in cryobiology occurred in 1949 with the accidental discovery of the cryoprotective properties of glycerol for human spermatozoa (Polge et al., 1949). This landmark study also identified the fine balance between protection and toxicity associated with the use of glycerol and other cryoprotectants such as propylene glycol and ethylene glycol. Progress in gamete cryobiology advanced quickly in those earlier years partly due to the ease of using post-thaw motility as a marker of retention of sperm function and the first birth following the use of human cryopreserved spermatozoa was soon demonstrated (Bunge et al., 1954). By the 1950s, the use of glycerol had also been explored in attempts to cryopreserve unfertilized oocytes (mouse: Sherman and Lin, 1959; sheep: Averill and Rowson, 1959)

1472-6483/$ - see front matter
doi:10.1016/j.rbmo.2010.10.018

and rabbit fertilized oocytes (Smith, 1953) with little success. A flurry of work aimed at unravelling the physiology of cell water movement and solidification of liquid water took place in the 1960s setting a foundation for future cryobiology (reviewed in Mazur, 1970). Sea urchin oocytes had proven useful in formulating these concepts (Asahina, 1961); however, successful preservation had only been reported with fertilized mouse oocytes (Whittingham et al., 1972). The potential benefits of stored mature oocytes over fertilized oocytes/embryos for immortalization of genetically inbred strains prompted the application of the procedure previously developed for mouse embryos with dimethylsulphoxide (DMSO) (Whittingham et al., 1972; Wilmut, 1972) to subzero freezing of mouse mature oocytes (Whittingham, 1977). Following the demonstration of good cryosurvival, comparable fertilization rates and the birth of live offspring reported by Whittingham, the procedure was subsequently used for rat (Kasai et al., 1979; Parkening and Chang, 1977), hamster (Critser et al., 1986; Parkening and Chang, 1977), rabbit (Diedrich et al., 1986; Siebzehnruebl et al., 1989) and primate (DeMayo et al., 1985) oocytes. The interrelationship between the development of cryobiology and knowledge of gamete physiology continued with the verification of theoretical models using the cryomicroscope stage and the mouse oocyte (an ideal cell due to size and spherical shape) (Bernard et al., 1988; Leibo, 1980; Leibo et al., 1978; Mazur et al., 1984). These studies clearly established the necessity for a slow cooling rate for oocytes and it is of interest to note that the rate of cooling applied in these and Whittingham's studies continue to be used for cryopreservation of oocytes and cleavage-stage embryos even today.

Concerns raised in animal oocyte cryopreservation studies

A number of concerns regarding the normality of embryos which developed from frozen oocytes were raised in the literature. Embryo and fetal development were consistently poor for mouse (Carroll et al., 1989; George et al., 1994; Glenister et al., 1987; Kola et al., 1988; Trounson and Kirby, 1989; Whittingham, 1977), rabbit (Al-Hasani et al., 1986) and hamster (Todorow et al., 1989a). The underlying problem was thought to be abnormalities in the meiotic spindle which appeared to be highly sensitive to reduced temperatures (Magistrini and Szollosi, 1980). This was confirmed in mouse oocytes by Pickering and Johnson (1987), who also observed that, on returning to 37°C, the spindle would frequently reform in an abnormal configuration with chromatids scattered in the ooplasm, establishing a possible mechanism for increased aneuploidy in cryopreserved oocytes. Genetic assessment of the resultant embryos supported this concept (Kola et al., 1988) although contrary results were obtained in similar studies (Glenister et al., 1987; Van der Elst et al., 1988). These latter studies did, however, identify another anomaly; an increase in the rate of polyploidy of digynic origin, an indication of parthenogenetic activation. Subsequent studies confirmed that temperature and duration of cryoprotectant exposure increased the rate of parthenogenetic activation in mouse oocytes (Carroll et al., 1989; Shaw and Trounson, 1989; Van der Elst et al., 1992a).

Other studies at the time raised concerns regarding potential fertilization of cryopreserved mature oocytes following observations of physical damage (Todorow et al., 1989a) and structural modifications (Carroll et al., 1990; Johnson, 1989; Johnson et al., 1988) to the zona pellicuda. A reduced population of cortical granules (Schalkoff et al., 1989; Vincent et al., 1990) indicated spontaneous release of cortical granules as the likely reason for failure to fertilize (Carroll et al., 1990; Wood et al., 1992), although this was subsequently found to be a consequence of either inappropriate culture conditions (Carroll et al., 1993; Vincent et al., 1991) or dehydration (Johnson, 1989; Trounson and Kirby, 1989) and not cryopreservation *per se*.

Development of vitrification

Coincident with the above evidence was the development of vitrification, which had been proposed as a cryopreservation method as early as 1937 (Luyet, 1937) but based solely on ultra-rapid cooling rates. The turning point occurred in 1985 with the development of an ice-free cryopreservation procedure for mouse embryos in a cryoprotectant solution capable of attaining a glass transition state (Rall and Fahy, 1985). The main issue regarding success with vitrification was the necessity to balance the cryoprotectant solutions to reduce toxicity (Fahy et al., 1987). Initial studies reported success with live young following mouse embryo vitrification (Rall et al., 1987). Success was also achieved in hamster (Critser et al., 1986) and germinal vesicle-stage mouse oocytes (Van Blerkom, 1989) together with live young from mature mouse oocytes (Nakagata, 1989). Critical to success was a very short duration of exposure to the vitrification solution (Shaw et al., 1992).

In an attempt to simplify the vitrification solution, a high concentration of a single cryoprotectant (DMSO) appeared suitable for both hamster and mouse oocytes (Wood et al., 1993); however, this was associated with high post-implantation loss (Liu et al., 1993). Again evidence of chromosomal scattering (Sathananthan et al., 1988b), elevated aneuploidy (Van Blerkom and Davis, 1994), increased incidence of chromosomal abnormalities (Shaw et al., 1991) and malformed fetuses (Kola et al., 1988) heralded an abrupt halt to vitrification of oocytes.

Alternative approach

By the end of the 1980s, there appeared sufficient consensus that the oocyte was too vulnerable to cryopreservation at the metaphase-II stage and animal work shifted to evaluating slow cooling of germinal vesicle oocytes. High survival could be achieved with mouse germinal vesicle oocytes (Candy et al., 1998, 1994; Van der Elst et al., 1993, 1992b) but some studies observed impaired subsequent development (Schroeder et al., 1990; Van der Elst et al., 1993, 1992b), suggesting no overall benefit could be gained by cryopreserving at the germinal vesicle compared with the metaphase-II stage. A similar conclusion was drawn for human germinal vesicle oocytes with the DMSO procedure (Mandelbaum et al., 1988a) and later with the propanediol (PROH) procedure (Baka et al., 1995; Toth et al., 1994a); however, one birth was reported (Tucker et al., 1998).

Human oocyte cryopreservation

To increase the clinical efficiency of IVF following ovarian stimulation, there was a clear advantage to be gained if excess oocytes/embryos could be successfully cryopreserved. This soon came to fruition with the first pregnancies and birth (Trounson and Mohr, 1983; Zeilmaker et al., 1984), from embryos frozen using DMSO as a cryoprotectant being reported. Soon after these reports, methodology using PROH and sucrose as cryoprotectants was shown to be more reliable and was adopted widely (Lassalle et al., 1985; Renard and Babinet, 1984b; Testart et al., 1986). The advent of human embryo freezing and storage, however, raised ethical issues in some sections of the community and, despite the concerns which had been raised by animal studies, this prompted interest in the possibility of clinical application of oocyte cryopreservation.

In 1986, Chen (1986) reported the first pregnancy, resulting in the birth of twins, following slow freezing/rapid thawing of human oocytes using DMSO. Due to restrictions on embryo cryopreservation, human oocyte cryopreservation was also being evaluated in Germany and this resulted in a singleton birth (Van Uem et al., 1987) and two pregnancies which subsequently aborted (Al-Hasani et al., 1987). In Chen's hands, the DMSO-based procedure (which differed from that used for mouse oocytes only by the use of a higher seeding temperature) resulted in 80% survival, 83% fertilization and 60% development to the 6–8-cell stage (Chen, 1986). However, attempts to replicate these results failed to achieve the reported levels of survival, fertilization and development (Al-Hasani et al., 1988, 1987; Mandelbaum et al., 1988a; Todorow et al., 1989b) although the same method was producing high survival rates for human pronuclear zygotes, a high proportion of which continued to develop (Siebzehnruebl et al., 1989; Todorow et al., 1989b). In addition and consistent with the animal studies, a high proportion of the thawed human oocytes which subsequently fertilized were polyploid (Al-Hasani et al., 1987; Mandelbaum et al., 1988b).

At this time, comparisons were also made to slow freezing with PROH, which had been shown to be less toxic for human embryos than DMSO (Renard et al., 1984a) and vitrification (using 3 mol/l DMSO). Only a small number of oocytes were cryopreserved with PROH (Al-Hasani et al., 1987; Mandelbaum et al., 1988b; Todorow et al., 1989b; Trounson, 1986) and results were variable. Results with DMSO-based vitrification seemed even more variable with survival ranging from 0% to 60% (Al-Hasani et al., 1987; Pensis et al., 1989; Trounson, 1986), but one of these studies reported a fertilization rate of 50%, with 50% of embryos developing to the 8-cell stage (Trounson, 1986). These inconsistent results, together with lingering concerns regarding normality following oocyte cryopreservation and the rapid momentum gained in the application of embryo cryopreservation, brought clinical oocyte cryopreservation to a halt.

Oocyte cryopreservation in the 1990s

Despite the cessation of clinical activity, human oocyte cryopreservation continued to be of interest to some groups. Although improvements in methodology achieved higher survival rates with the DMSO procedure for both mouse and human oocytes, human oocytes failed to progress past fertilization (Hunter et al., 1991). At this time, the PROH method developed by Renard and Babinet (1984b) which had been modified to include 0.1 mol/l sucrose to aid in dehydration was being assessed (Lassalle et al., 1985). In the initial experience, the procedure was detrimental to mouse unfertilized oocytes but pronuclear mouse zygotes survived well and formed blastocysts (Gook et al., 1993). These conflicting results could be explained by the different water permeability kinetics before and after fertilization in mouse oocytes (Orrico et al., 1988). The similarity in the estimated water permeability for the mouse pronuclear zygote and the human metaphase-II oocyte (Bernard et al., 1988) led to this procedure being assessed with the human oocyte. An immediate post-thaw survival rate of over 60% was observed although gradual deterioration of the oolemma in some oocytes reduced survival to 54% (Gook et al., 1993). In contrast to all previous studies, survival was assessed on a large number (171) of randomly donated human oocytes. A negative impact on survival was observed with in-vitro ageing prior to cryopreservation ($>$6 h) and cryopreservation within the cumulus mass, which was in contrast to previous observations (Imoedemhe and Sigue, 1992; Mandelbaum et al., 1988b). The robust nature of the procedure was established by similar survival rates in two other series of oocytes (134 and 46 oocytes; Gook et al., 1995b, 1994).

Of course, survival itself would be irrelevant if normal developmental potential had been compromised. Neither exposure to the cryoprotectants (at about 20°C) nor cryopreservation significantly increased abnormalities of the spindle (Gook et al., 1993) in agreement with the previous suggestion of a protective action of PROH on the spindle (Van der Elst et al., 1988). The observation of an abundance of cortical granules within the oocyte and no evidence of release from the oolemma suggested that potential for fertilization was unimpaired (Gook et al., 1993). Confirming this suggestion, a similar normal fertilization rate to that for non-frozen oocytes inseminated with the same sperm preparation was observed for the cryopreserved oocytes with no increase in haploidy or polyploidy (Gook et al., 1994). Normal and abnormal fertilization rates of 50% and $<$10%, respectively, following insemination were verified with a second group of cryopreserved oocytes (Gook et al., 1995b). It was also shown that the elevated rate of polyploidy previously reported (Al-Hasani et al., 1987) was a consequence of ageing and not cryopreservation (Gook et al., 1995a, 1994) and further demonstrated that the risk of digynic parthenogenetic activation was low (Gook et al., 1995a).

Concerns relating to the likelihood of a high rate of aneuploidy in cryopreserved human oocytes were alleviated by the absence of stray chromatin or micronuclei in over 140 oocytes examined after cryopreservation (Gook et al., 1994). The next challenge was to determine whether normal embryo development was possible. Due to legislation prohibiting embryo research in Victoria, Australia, these studies were conducted at two other centres. At one of the centres, intracytoplasmic sperm injection (ICSI) (Palermo et al., 1992) was being developed for clinical use and a comparison of insemination and ICSI of cryopreserved oocytes was carried out. Embryo development to the blastocyst stage was observed with both types of fertilization although

faster development was noted and more embryos continued development following ICSI (Gook et al., 1995b). In 1994, the world's first egg bank was started at the Royal Women's Hospital, Melbourne, providing an option to preserve fertility for young women with malignant disease. Although of clinical importance in these circumstances, the time between cryopreservation and thawing for this group of patients was likely to be considerable leading to delay in obtaining any information on clinical outcomes from cryopreserved oocytes. This situation, together with the imminent changes to the Italian law which would preclude embryo cryopreservation, prompted collaboration with the group in Bologna and culminated in the first birth with the PROH procedure in 1997 (Porcu et al., 1997). Previous to this, three pregnancies had been initiated using the PROH procedure and, although none had continued to term, normal karyotype was indicated (Tucker et al., 1996). By the end of the 1990s the Bologna group (Porcu et al., 1999 1998) and and a number of others had established pregnancies and births with the procedure (Antinori et al., 1998; Borini et al., 1998; Nawroth and Kissing, 1998; Polak de Fried et al., 1998; Tucker et al., 1998; Wurfel et al., 1999; Young et al., 1998).

Improvements in slow cooling

It became apparent during the early stages of clinical application that there was a large variation in response to the PROH/0.1 mol/l sucrose procedure between oocytes, possibly explicable by an important observation of a five-fold variation in water permeability kinetics between individual mature human oocytes (Hunter et al., 1992). To facilitate water movement, increasing the sucrose concentration was suggested as a possible solution. Although the use of 0.2 mol/l sucrose improved survival relative to 0.1 mol/l sucrose (Chen et al., 2004; Fabbri et al., 2001), additional improvement appeared to be achieved by further increasing the sucrose concentration to 0.3 mol/l (Fabbri et al., 2001). With proclamation of the Italian Law approaching, numerous Italian groups quickly adopted the 0.3 mol/l sucrose procedure clinically. However, from a number of studies published in 2006–2007 (reviewed in Gook and Edgar, 2007), it appeared that the implantation potential of the resultant embryos was compromised using the 0.3 mol/l sucrose method. Again spindle damage was implicated but numerous studies, using more advanced technologies than previously available – the Polscope (Bianchi et al., 2005a; Rienzi et al., 2004) and confocal microscopy (Cobo et al., 2008a; Coticchio et al., 2010, 2006; De Santis et al., 2007) – found this not to be the case. The reduced implantation with the 0.3 mol/l sucrose was associated with retarded cleavage (Bianchi et al., 2005b; Borini et al., 2006) due to perturbations of the cytoplasm (Nottola et al., 2007) and degeneration of mitochondria (Gualtieri et al., 2009).

During this time, the 0.2 mol/l sucrose procedure with dehydration at 37°C was used by a small number of groups (Bianchi et al., 2007; Gook et al., 2007; Winslow et al., 2001; Yang et al., 2002, 1998). Although no comparative clinical studies were performed with 0.2 mol/l and 0.3 mol/l sucrose procedures, embryo development following fertilization of oocytes cryopreserved in 0.2 mol/l sucrose was similar to fresh oocytes (Coticchio et al., 2007) and no impact on the implantation rate was observed (Bianchi et al., 2007).

Another approach introduced in human oocyte cryopreservation was the removal of sodium from the cryopreservation media, which had been shown to result in high survival (>90%) and pregnancy rates with mouse oocytes (Stachecki et al., 2002, 1998). This was initially introduced clinically with 0.1 mol/l sucrose (Quintans et al., 2002) and later used with higher sucrose concentrations (Boldt et al., 2006; Petracco et al., 2006); all procedures resulting in small numbers of births. The substitution of sodium with choline did not appear to adversely affect fertilization or the proportion of embryos which subsequently cleaved, but retarded development was observed (Petracco et al., 2006).

Clinical introduction of vitrification

Shortly after the first birth from slow cooling of oocytes, the first pregnancy (Cha et al., 1999) and birth (Kuleshova et al., 1999) from vitrified oocytes were reported. For some time prior to these reports, the critical parameters for vitrification had been under investigation. It was becoming apparent that reducing the duration of exposure to vitrification solutions reduced the toxicity (Ishimori et al., 1993). This appeared to improve survival of human oocytes when vitrified using the cryoprotectant mixture of Rall and Fahy (1985) but development halted at fertilization (Hunter et al., 1995). As had been the case with slow cooling, there was a transition from DMSO-based vitrification solutions in favour of another cryoprotectant; ethylene glycol (EG). This was based on an extensive evaluation of combinations of cryoprotectants by Ali and Shelton (1993). The high EG (5.5 mol/l) and sucrose (1 mol/l) solution developed by Ali and Shelton proved successful for bovine (Martino et al., 1996) and murine (Hotamisligil et al., 1996) oocytes and human cleavage-stage embryos (Mukaida et al., 1998) and resulted in the above pregnancies from human oocytes and a further seven births by 2003 (Yoon et al., 2003). Concomitant with these advances was the development of appropriate carriers to facilitate the speed of cooling necessary. These included open-pulled straws (Vajta et al., 1998), electron microscopy grids (Martino et al., 1996) and nylon loops (Lane et al., 1999). This area has been extensively reviewed by Vajta and Nagy (2006).

Guided by Rall and Fahy's original philosophy of using a combination of cryoprotectants to reduce individual toxicity, others were assessing various cryoprotectant cocktails. The combination of EG and DMSO reported for mouse (Ishimori et al., 1992) and bovine embryos (Ishimori et al., 1993), together with sucrose (Vajta et al., 1998), would later be the basis of the vitrification revolution in assisted reproduction treatment. By the end of the 1990s, vitrification was being applied to human embryos and successfully achieving pregnancies with blastocysts (Vanderzwalmem et al., 1997) and births with cleavage-stage embryos (Hsieh et al., 1999).

For human oocytes, both the use of a single permeating cryoprotectant (EG) (Chen et al., 2000; Kuwayama and Kato, 2000; Wu et al., 2001; Yoon et al., 2002) and the use of combinations of permeating cryoprotectants (EG + DMSO) (Liebermann et al., 2003; Vanderzwalmem et al., 2000) together with sucrose continued to be investigated.

However, the major obstacle restricting clinical application for both embryos and oocytes was the lack of an appropriate carrier. The introduction of the cryotop, developed in Japan, was pivotal to subsequent success with vitrification. By achieving an extremely rapid-cooling rate, facilitated by minimal fluid volume, survival rates of over 90% and the establishment of live births were reported (Katayama et al., 2003; Kuwayama et al., 2005; Kyono et al., 2005; Okimura et al., 2005). Due to its technically challenging nature, the Cryotop, in conjunction with the EG/DMSO/sucrose procedure, was originally slow to gain widespread acceptance for oocyte vitrification (Lucena et al., 2006; Selman et al., 2006). However, following minor methodological modifications, two large comparative studies (Antinori et al., 2007; Cobo et al., 2008b) cemented its place in oocyte cryopreservation history. At the same time, development of a similar procedure in which DMSO was replaced with PROH in conjunction with the use an alternative carrier, the Cryoleaf, was reported (Chian et al., 2009, 2005).

By 2008, the poor implantation rates observed with the 0.3 mol/l sucrose slow-freezing method were being contrasted to the demonstration of outcomes from vitrified oocytes which were similar to those from fresh oocytes. This led to a widespread shift to vitrification by many groups in Italy where the majority of oocyte cryopreservation was occurring. However, in some programmes, which had achieved good success with slow freezing, both slow freezing and vitrification are used in parallel with approximately equivalent success and outcomes similar to those from fresh oocytes (Noyes et al., 2010a). At present, equal numbers of babies have been born from both techniques (Noyes et al., 2009), altogether exceeding over 900 babies born, with live-birth outcomes similar to those occurring following conventional IVF. It would appear that there is a role for both procedures today and in the future.

Conclusion

The acceptance of oocyte cryopreservation in general assisted reproduction practice has finally come to fruition, having answered many of the criticisms raised during a chequered past. It has now arrived at a stage where it is considered as routine in some oocyte donation programmes (Cobo et al., 2010, 2008b) and as a fertility preservation option for young women with cancer (Noyes et al., 2010b; Porcu et al., 2008; Yang et al., 2007). The success of oocyte cryopreservation, demonstrated by over 900 births, and the reassurance provided by no apparent increase in birth anomalies relative to conventional IVF (Noyes et al., 2009) have cemented its position in routine treatment. Although it may have taken over 30 years to reach this point, the success rates today indicate that oocyte cryopreservation may soon be considered as an alternative to embryo cryopreservation in appropriate circumstances.

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Declaration: The author reports no financial or commercial conflicts of interest.

Received 13 August 2010; refereed 28 September 2010; accepted 27 October 2010.