Chapter 7
Effect of metachronal waves

Abstract

In this chapter we study the effect of metachronal waves on the flow created by magneto-driven artificial cilia in microchannels. We use a coupled magneto-mechanical solid-fluid model that captures the physical interactions between the fluid flow, ciliary deformation and applied magnetic field. When a rotating magnetic field is applied to super-paramagnetic artificial cilia, they mimic the asymmetric motion of natural cilia, consisting of an effective and recovery stroke. Two ways of generating a metachronal motion of cilia are considered; by prescribing an external phase difference and by applying a non-uniform magnetic field. We show that the fluid flow created by the artificial cilia is significantly enhanced in the presence of metachronal waves and that the fluid flow becomes unidirectional. Antiplectic metachrony is observed to lead to a considerable enhancement in flow compared to symplectic metachrony, when the cilia spacing is small. Obstruction of flow in the direction of the effective stroke for the case of symplectic metachrony was found to be the key mechanism that governs this effect.

7.1 Introduction

The control of fluid flow in channels of micron-scale dimensions is essential for proper functioning of any lab-on-a-chip device. The fluid transport in microchannels is often performed by downscaling conventional methods such as syringe pumps, micropumps (Laser & Santiago, 2004; Jeon et al., 2000; Schilling et al., 2002), or by exploiting electromagnetic fluid manipulation principles, as in electro-osmotic (Chen et al., 2003; Zeng et al., 2002) and magneto-hydrodynamic (West et al., 2002) devices. In search for novel ways to propel fluids at micron scales, we let nature be our guide. Nature uses hair-like structures, called cilia, attached to the surfaces of microorganisms, to propel fluids at small length scales. The typical length of a cilium is 10 microns. Cilia beat in a whip-like asymmetric manner consisting of an effective stroke and a recovery stroke. Moreover, when many cilia operate together, hydrodynamic interactions cause them to beat out-of-phase (Gueron et al., 1997), leading to the formation of metachronal waves, and an enhanced fluid flow (Satir & Sleigh, 1990). The specific metachrony is termed symplectic (or antiplectic) when the metachronal wave is in the same (or opposite) direction as the effective stroke. The cilia on a Paramecium exhibit antiplectic metachrony, whereas the cilia on Opalina exhibit symplectic metachrony (Blake, 1972).

The asymmetric motion of natural cilia is due to the intricate interaction between the cilia microstructure (axoneme) and the internal driving force generated by ATP-enabled conformational changes of the motor protein dynein. It is a challenging task to design the artificial counterpart of natural cilia, by using external force fields for actuation in order to mimic the asymmetric motion of natural cilia. An early attempt to create artificial cilia was based on electrostatic actuation of cilia-like microactuator arrays (den Toonder et al., 2008). Although effective flow and mixing were achieved, movement of these artificial cilia was not asymmetric as in the case of natural cilia. It was predicted using numerical simulations that an array of identical super-paramagnetic or permanently magnetic two-dimensional plate-like cilia can mimic the planar asymmetric motion of natural cilia when exposed to a uniform magnetic field (Khaderi et al., 2009). These magnetic artificial cilia can be realised, for instance, by using polymer films with embedded super-paramagnetic (or permanently magnetic) nano-particles (see e.g. Fahrni et al., 2009; Belardi et al., 2010; Schorr et al., 2010). In contrast with the plate-like cilia, rod-like structures that mimic the three-dimensional motion of nodal cilia to create fluid propulsion have also been fabricated (Vilfan et al., 2010; Shields et al., 2010; Evans et al., 2007). In (Sing et al., 2010), a novel method of fluid propulsion based on magnetic walkers was presented. Artificial cilia based on photo-actuation have also been realised in the recent past (van Oosten et al., 2009).

In previous studies we focused on the flow created by an array of synchronously-beating cilia whose motion is planar and asymmetric, in the absence (Khaderi et al., 2009) and presence of fluid inertia (Khaderi et al., 2010). Using numerical simulations it was reported that a substantial but fluctuating flow is created in the former, while in the latter the flow increases significantly as the Reynolds number is increased. In addition, the fluid flow can become unidirectional in the presence of fluid inertia. In this work we explore another aspect of natural ciliary propulsion - the metachronal motion of cilia, by allowing the asymmetrically-beating artificial cilia to move out-of-phase. The out-of-phase motion of the cilia is achieved by applying a magnetic field that has a phase lag between adjacent cilia. The existing literature on the metachronal motion of natural cilia could provide insights on the flow generated in the presence of metachronal waves.

In the case of natural cilia the metachronal motion is analysed principally for two reasons. First, to find the effect of the metachronal waves on the flow created and second, to find the physical origin of the metachronal waves. Theoretical and numerical studies have been undertaken by biologists and fluid mechanicians to understand the flow created by an array of cilia (see for e.g. the reviews by Brennen & Winet, 1977; Blake & Sleigh, 1974; Smith et al., 2008). Most of these analyses have been performed to model the flow of specific biological systems (e.g. microorganisms or airway cilia), however, a systematic study is lacking. In the following, we outline a number of studies in which the effect of the metachronal waves on fluid transport has been studied. Modelling approaches to understand the cilia-driven flow include the envelope model (Brennen & Winet, 1977; Blake, 1971a,c), the sublayer model (Blake, 1972; Guerou et al., 1997; Smith et al., 2007; Liron, 1978; Gauger et al., 2009; Gueron & Levit-Gurevich, 1999), fluid-structure interaction models using a lattice-Boltzmann approach (Kim & Netz, 2006), and the immersed boundary method (Dauplain et al., 2008). In the envelope model, the cilia are assumed to be very densely spaced so that the fluid experiences an oscillating surface consisting of the tips of the cilia. The envelope model is accurate only when the cilia are spaced very close together, which has only been observed in the case of symplectic metachrony (Blake, 1971a,c). In the sublayer model (Blake, 1972),
the cilia are represented by a distribution of Stokeslets with appropriate mirror images to satisfy the no-slip condition on the surface to which the cilia are attached. The sublayer model predicts that for an organism that exhibits antiplectic metachrony, the flow created is lower than for cilia beating in-phase. In the case of an organism exhibiting symplectic metachrony, the opposite trend is observed. In the numerical study of (Gauger et al., 2009), the flow due to the out-of-phase motion of a finite number of magnetic cilia subjected to an oscillating external magnetic field was studied. The magnetic cilia generate an asymmetric motion due to the difference in the speed of oscillation of the magnetic field during the effective and recovery strokes. In contrast to (Blake, 1972), it was predicted that the flow in the case of antiplectic metachrony is larger than the flow created by a symplectic metachrony for a particular inter-cilia spacing.

Early experiments indicated that the hydrodynamic coupling between cilia could be the cause for the formation of the metachronal waves (see for e.g. the review by Kinosita & Murakami, 1967). By mimicking the ciliary motion of Paramecia using an internal actuation mechanism, it was demonstrated that cilia, which were initially beating in-phase, will form an antiplectic metachronal wave after a few beat cycles (Gueron et al., 1997). This behaviour was explained to be an outcome of the hydrodynamic interactions between neighbouring cilia. Similar hydrodynamically-caused metachronal motion of the cilia was also observed by (Mitran, 2007). In (Gueron & Levit-Gurevich, 1999), it was reported that in the presence of the metachronal wave the cilia become more efficient in creating flow. The synchronization and phase locking of the cilia have also been analysed using simple experimental (Qian et al., 2009) and analytical (Niedermayer et al., 2008; Vilfan & Jülicher, 2006) models. It was found that some degree of flexibility is required for the phase locking of the cilia to take place (Niedermayer et al., 2008; Qian et al., 2009). The requirement of the flexibility for synchronization is also confirmed from the more detailed model of (Kim & Netz, 2006). In the aforementioned studies, however, the metachronal wave is an outcome of that specific system, and the flow or the efficiency has not been studied for different types of metachronal waves.

The goal of this chapter is, therefore, to obtain a full understanding of the dependence of flow on the magnetically-induced out-of-phase motion of an array of asymmetrically beating artificial cilia. We will answer the following questions using a coupled solid-fluid magneto-mechanical model. How does the generated flow in the presence of metachrony differ from the flow generated by cilia that beat in-phase? How does the flow depend on the metachronal wave speed and its direction, and how does it depend on the cilia spacing? We answer these questions in the light of magnetic artificial cilia which exhibit an asymmetric motion and beat out-of-phase. However, the results are equally applicable to any ciliary system in which the cilia exhibit an asymmetric and out-of-phase motion.

The out-of-phase motion of artificial cilia can be achieved by applying a non-uniform magnetic field that travels in space and time. However, a non-uniform magnetic field will also cause magnetic body forces to act on the cilia, which will lead to a beat motion that is different compared to that of synchronously beating cilia. Therefore, we study the out-of-phase motion of the cilia in two steps. First, we apply a rotating magnetic field that is uniform over each cilia but has a phase difference between neighbouring cilia. This keeps the asymmetric motion of the cilia nearly unaltered, and enables us to identify the physical mechanisms that are operative when the cilia beat out-of-phase. In the second step, we apply a non-uniform magnetic field to the cilia and study how the body forces influence the beat motion of the cilia and the resulting flow.

The chapter is organised as follows. The boundary value problem and the solution
Fig. 7.1: (a) Schematic representation of the problem analysed. We study an infinitely long microfluidic channel consisting of equal-sized cilia spaced a distance $a$ apart. The variation of magnetic field in space is shown using blue arrows. $Q_p$ and $Q_n$ denote the flow in the direction of the effective and recovery stroke, respectively. (b) Typical asymmetric motion of a cilium. The dashed lines represent the trajectory of the tip of an individual cilium.

Methodology are explained in section 7.2.1. In section 7.2.1, the physical mechanisms responsible for the enhanced flow in the presence of metachronal waves are discussed. The quantitative variation of the flow as a function of the phase difference and cilia spacing is given. The deformation of the cilia due to the non-uniform magnetic field and the resulting flow are studied in section 7.2.2. Finally, the outcome of the analysis is summarised in section 7.3.

### 7.2 Results

#### 7.2.1 Externally imposed out-of-phase motion

We study the flow in an infinitely long channel of height $H$ created by a two-dimensional array of magnetic artificial cilia, which are actuated using a rotating magnetic field which is uniform over each cilium, but with a phase difference between adjacent cilia. The external magnetic field experienced by the $i$th cilium is

$$B_{x_i} = B_0 \cos(\omega t - \phi_i), \quad B_{y_i} = B_0 \sin(\omega t - \phi_i),$$  \hspace{1cm} (7.1)$$

where $B_0$ is the magnitude of the applied magnetic field, the phase of the magnetic field $\phi_i = 2\pi(i-1)/n$, $\omega = 2\pi/t_{\text{ref}}$ is the angular frequency and $t_{\text{ref}}$ is the time period of rotation of the magnetic field. The magnetic field experienced by the individual cilia during a particular instance in time is shown using the blue arrows in Fig. 7.1(a). The phase difference in the applied magnetic field between adjacent cilia is $\Delta\phi = 2\pi/n$. The chosen form of the phase $\phi_i$ makes the phase of the magnetic field at every $n$th cilium identical. That is, the magnetic field is periodic after $n$ repeats of cilia. Consequently, the applied magnetic field travels $n$ cilia units in time $t_{\text{ref}}$, so that the phase velocity of the magnetic field is $n/t_{\text{ref}} = \omega/\Delta\phi$ (in cilia per second). The phase velocity is to the right (positive) and the magnetic field at each cilium position rotates counterclockwise with time. The typical asymmetric motion of a cilium is shown in Fig. 7.1(b). The cilia are tethered at one end to the surface, while the other end is free. The trajectory of the free end of a typical cilium is represented by the dashed lines in Fig. 7.1(b), with the arrows representing the direction of motion.
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Due to the super-paramagnetic (SPM) nature of the cilia, for which the magnetization is proportional to the magnetic field, the magnetic body couple \( \mathbf{N} = \mathbf{M} \times \mathbf{B}_0 \), where \( \mathbf{M} \) is the magnetization of the cilia and \( \mathbf{B}_0 = (B_x, B_y) \) is the magnetic field experienced by the cilia) depends only on the orientation and magnitude of the magnetic field, but not on its sign. As a result, the body couple at the \( i^{th} \) cilium \( N_{zi} \), which determines its motion, scales with \( \sin(2\omega t - 2\phi_i) \) (see Eqn. 2.37). This has consequences for the motion of the cilia, both temporally and spatially. Temporally, the frequency of the magnetic couple is twice that of the applied magnetic field. This results in two cilia beats for one \( 360^\circ \) rotation of the magnetic field. Spatially, the phase of the magnetic couple is twice that of the applied magnetic field, so that the phase difference between neighbouring cilia is twice as large. This means that the magnetic couple is periodic after \( n/2 \) cilia. Since both the frequency and phase difference increase by a factor 2, the phase velocity of the magnetic torque remains equal to that of the magnetic field, i.e. \( \omega/\Delta\phi \). Note, however, that the phase velocity of the magnetic torque is equal to the velocity of the metachronal wave (i.e., the actually observed deformational wave travelling over the cilia) only when the phase difference \( \Delta\phi \) is small (i.e. \( n \) is large).

When the phase difference is too large, the metachronal wave can change sign, so that the metachronal wave is observed to travel in a direction opposite to the direction of the magnetic field (see appendix J). The metachronal wave velocity is equal to \( \omega/\Delta\phi \) (i.e. to the right) when \( 0 < \Delta\phi < \pi/2 \), and it is equal to \( -\omega/(\pi - \Delta\phi) \) (i.e. to the left) when \( \pi/2 < \Delta\phi < \pi \), see Fig. 7.2. When \( \Delta\phi = 0 \), the magnetic couple is uniform and all cilia beat in-phase. When \( \Delta\phi = \pi \), the magnetic couple acting on two neighbouring cilia is the same (because the phase difference of the magnetic couple is \( 2\Delta\phi = 2\pi \)), and again, all the cilia beat in-phase. When \( \Delta\phi = \pi/2 \), the positive metachronal wave velocity is equal in magnitude to its negative counterpart. In such a condition, a standing wave is observed which causes the adjacent cilia to move in anti-phase. When \( 0 < \Delta\phi < \pi/2 \) the metachronal wave velocity is positive, i.e. to the right in Fig. 7.1. Consequently, the metachronal wave velocity is opposite to the direction of the effective stroke, which is commonly addressed as antiplectic metachrony (AM). When \( \pi/2 < \Delta\phi < \pi \), the metachronal wave velocity is in the same direction as the effective stroke and is referred to as symplectic metachrony (SM), see Fig. 7.2.

We model the cilia as elastic Euler-Bernoulli beams taking into consideration geometric non-linearity and inertia of the cilia in a Lagrangian framework. The magnetic field is calculated by solving the Maxwell’s equations using a boundary element approach for each ciliary configuration (see chapter 2). The Stokes equations, which capture the behaviour of the fluid flow at low Reynolds numbers, are solved within an Eulerian setting for the velocity and pressure using finite elements. The velocity is interpolated quadratically, while the pressure is interpolated linearly within each element. The solid-fluid coupling is performed by imposing the no-slip condition at the nodal points of the Euler-Bernoulli beam elements using Lagrange multipliers (point collocation method) within a fictitious domain framework (van Loon et al., 2006). The solution procedure is as follows. The Maxwell’s equations are solved at every time instant to solve for the magnetic field. From the magnetic field, the magnetic body couple acting on the cilia is calculated and is provided as an external load to the implicitly-coupled solid-fluid model, which simultaneously solves for the cilia velocity, and the velocity and pressure of the fluid. The velocity of the cilia is integrated using Newmark’s algorithm to obtain its new position, and the procedure is repeated. For more details on the numerical model the reader is referred to chapter 2. Each cilium is discretised into 40 elements and every fluid
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![Graph showing metachronal wave velocity as a function of phase difference \( \Delta \phi \) in units of \( \pi \). The graph illustrates the velocity in units of \( \omega/\pi \) with phase differences ranging from -10 to 10.

The physical dimensionless numbers that govern the behaviour of the system are the magneto-elastic number \( M_n = 12B_0^2L^2/\mu_0 Eh^2 \) - the ratio of the magnetic to the elastic forces, the fluid number \( F_n = 12\mu L^3/Eh^2t_{beat} \) - the ratio of viscous forces acting on the cilia to the elastic forces, and the inertia number \( I_n = 12\rho L^4/Eh^2t_{beat}^2 \) - the ratio of the inertia forces of the cillum to its elastic forces, (see Khaderi et al., 2009). Here, \( E \) is the elastic modulus of the cillum, \( h \) is the thickness, \( \rho \) is the density of the cillum, \( \mu \) is the fluid viscosity, \( t_{beat} (= t_{ref}/2) \) is the time period of one beat cycle and \( \mu_0 \) is the magnetic permeability. The geometric parameters that govern the behaviour of the system are the phase difference \( \Delta \phi \), the cillum spacing \( a \), their length \( L \) and the height of the channel \( H \). We study the flow created as a function of the cillum spacing \( a \) (normalised with the length \( L \)) and the phase difference \( \Delta \phi \) for the following set of parameters: \( F_n = 0.15 \), \( M_n = 12.2 \), \( I_n = 4.8 \times 10^{-3} \) and \( H/L = 2 \). The values of the physical parameters correspond to \( L = 100 \) microns, \( E = 1 \) MPa, the thickness of cillum being \( h = 2 \mu m \) at the fixed end and \( 1 \mu m \) at the free end, \( \rho = 1600 \) kg/m\(^3\), \( \mu = 1 \) mPas, \( B_0 = 22.6 \) mT and the cycle time \( t_{ref} = 20ms \). The magnetic susceptibilities of the cillum are 4.6 along
the length and 0.8 along the thickness (van Rijsewijk, 2006).

The fluid propelled is characterised by two parameters: the net volume of the fluid transported during a ciliary beat cycle and the effectiveness. The horizontal velocity field in the fluid at any $x$ position, integrated along the channel height gives the instantaneous flux through the channel. This flux integrated in time over the effective and recovery stroke gives the positive ($Q_p$) and negative ($Q_n$) flow, respectively (see Fig. 7.1). Due to the asymmetric motion, the positive flow is larger than the negative flow, generating a net area flow per cycle ($Q_p - Q_n$) in the direction of the effective stroke. The effectiveness, defined as $(Q_p - Q_n)/(Q_p + Q_n)$, indicates which part of the totally displaced fluid is effectively converted into a net flow. An effectiveness of unity represents a unidirectional flow. For each value of $a/L$, we choose $n$ to be a fraction $p/q$ larger than 2, with $p$ and $q$ integers, yielding a range of phase differences $\Delta \phi = 2\pi/n$ between 0 and $\pi$. For each value of $p/q$, a unit-cell of width $W = pa$ needs to be chosen to account for periodicity in the magnetic couple, unless $p$ is an even integer, for which $W = pa/2$ suffices. For example, let $p = 10$ and $q = 3$. Now, $n = 10/3$ and the phase difference $\Delta \phi$ is equal to $3\pi/5$. To maintain periodicity in the magnetic couple, the width of the unit-cell should be $5a$ (containing 5 cilia). The top and bottom of the unit-cell are the channel walls, on which no-slip boundary conditions are applied, while the left and right ends are periodic in velocity.

**Results and discussion**

To obtain an understanding of fluid flow due to the out-of-phase motion of cilia, we analyse the case of antiplectic metachrony with a phase difference $\Delta \phi = 2\pi/n = 2\pi/12$. Since $n$ is even, a unit-cell of width $6a$ consisting of 6 cilia is chosen, see Fig. 7.4. The contours represent the absolute velocity normalised with $L/t_{beat}$. The direction of the velocity field can be determined from the arrows on the streamlines. The white arrows represent the applied magnetic field for each cilium.

The snapshots shown in Figs. 7.4(a)-7.4(f) correspond to the time instances when the flux generated by the cilia is maximum. In Fig. 7.4(g) the instantaneous flux as a function of time $t$ (right axis) in addition to the flow (accumulated flux at time $t$, left axis) are plotted. The time instances corresponding to Figs. 7.4(a)-7.4(f) are marked in Fig. 7.4(g). The motion of the fluid particles near the third cilium under the influence of the velocity field caused by the ciliary motion is also shown. It can be observed from Fig. 7.4(g) that one beat cycle consists of six sub-beats, which correspond to the traveling of the magnetic couple from one cilium to the next. The traveling of the metachronal wave to the right can, for instance, be seen by looking at the cilia which exhibit the recovery stroke (i.e. cilium 1 in Fig. 7.4(a), cilium 2 in Fig. 7.4(b), etc). The negative flow created by the cilia during their recovery stroke is overcome by the flow due to the effective stroke of the rest of the cilia; this leads to a vortex formation near the cilia exhibiting their recovery stroke. As a result, the negative flow is completely obstructed for most of the time during the recovery stroke. It can be observed from Fig. 7.4(g) that no flux (right axis) is transported in the negative direction, and that the flow (left axis) continuously increases during each sub-beat. Moreover, the increase in the flow during each sub-beat is similar (see Fig. 7.4(g)). Thus, the total flow per beat cycle (left axis of Fig. 7.4(g)) is the sum of the flows generated during each sub-beat (i.e. flow per beat $= 6 \times$ flow generated during one sub-beat). Therefore, it is sufficient to analyse the fluid flow during one sub-beat.
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Figure 7.4: (a)-(f) Out-of-phase motion of cilia during a representative cycle for $\Delta \phi = \pi/6$ ($n = 12$) with the wave moving to the right (antiplectic metachrony) for $a/L = 1.67$. The contours represent the absolute velocity normalised with $L/t_{\text{beat}}$. The direction of the velocity is represented by streamlines. The white circles represent fluid particles. The applied magnetic field at each cilium is represented by the white arrows. (g) Instantaneous flux (right axis) and flow (or accumulated flux, left axis) as a function of time with the instants (a)-(g) duly marked.

In the following, we analyse the fluid motion and the resulting flow during the second sub-beat. The velocity profiles at different instants of this sub-beat are shown in Figs. 7.5(a)-7.5(d). The corresponding flow and the flux generated are shown in Fig. 7.5(e). At $t_{\text{beat}}/6$, the third cilium starts its recovery stroke and the particles near the top boundary are driven by the positive flow created by cilia 4, 5 and 6 (see Fig. 7.5(a)). At this instant, as only one cilium is exhibiting a recovery stroke, the flux created by the cilia is maximum (see instant ‘a’ in Fig. 7.5(e)). In Fig. 7.5(b), the third cilium also has begun its recovery stroke and now the negative flow caused by both the
second and third cilia is opposed by the effective stroke of the other cilia. The high velocity of the second cilium during its recovery stroke decreases the flux caused by the other cilia (see instant ‘b’ in Fig. 7.5(e)). When the third cilium is half-way through its recovery stroke (see Fig. 7.5(c)), the second cilium is about to finish its recovery, which generates a large velocity, due to the whip-like action (Khaderi et al., 2009), to the right. Now, the position of the third cilium is such, that it opposes the negative flow caused by the second cilium. This leads to a strong vortex formation near the second and third cilia, with only a small flux in the direction of the recovery stroke (to the right). The small negative flux caused by the whip-like motion of the second cilium can be seen by the instant marked ‘c’ in Fig. 7.5(e), causing a momentary decrease in the flow. The vortex imparts a high velocity in the direction of the effective stroke to the particles away from the cilia. As the third cilium progresses further in its recovery stroke, the particles come under the influence of the flow due to the rest of cilia, which are now in different phases of their effective stroke (see Fig. 7.5(d)). Now, only the third cilium is in the recovery stroke; this again leads to a maximum value of the flux (similar to Fig. 7.5(a)).

The key observation of Figs. 7.4 and 7.5 is that the negative flow created during the recovery stroke of the cilia creates a local vortex due to the positive flow created by other cilia. This shielding effect during the recovery stroke leads to a drastic increase in the net propulsion rate for cilia beating out-of-phase, compared to synchronously beating cilia.

Next, we analyse the instantaneous flux (Fig. 7.6(a)) and flow generated (Fig. 7.6(b)) as a function of time for different phase differences. When the cilia move synchronously ($\Delta \phi = 0$), the flux (see the solid line in Fig. 7.6(a)) is positive for approximately three-quarters of the time and strongly negative during the rest of the cycle. Consequently, the flow generated (see the solid line in Fig. 7.6(b)) increases during the effective stroke, but profoundly decreases when the recovery stroke takes place. This creates a large fluctuation in the flow, with only a small net amount of fluid transported. Once the ciliary motion is metachronal, the negative flux is very small compared to the positive flow (see the cases of a standing wave and antiplectic metachrony in Fig. 7.6(a)). This decreases the fluctuation in the flow generated, causing it to increase nearly monotonously during the beat cycle (see the dashed and dotted lines in Fig. 7.6(b)). We can clearly see that the flow at the end of the beat cycle ($t = t_{\text{beat}}$) for out-of-phase motion is significantly larger than the flow created by the synchronously beating cilia.

The fluid propelled and the corresponding effectiveness are plotted for different values of $\Delta \phi$ and $a/L$ in Fig. 7.7. The metachronal wave velocity (Fig. 7.2) is plotted as a function of $\Delta \phi$ and is shown using dashed lines in Fig. 7.7(a). As mentioned earlier, when the metachronal wave velocity is positive an antiplectic metachrony (AM) results, and when the metachronal wave velocity is negative we get a symplectic metachrony (SM). When all the cilia are moving synchronously ($\Delta \phi = 0$ or $\pi$), the flow (normalised by $\pi L^2/2$) will be approximately 0.22 for $a/L = 5$. As the cilia density is increased by decreasing $a$ from $a/L = 5$ to $a/L = 1.67$, the viscous resistance per cilium decreases, which causes the normalised flow to increase to 0.25. When the cilia beat in-phase, the effectiveness of fluid propulsion is very low, see Fig. 7.7(b). The fluid propelled shows a substantial increase once the cilia start beating out-of-phase (Fig. 7.7(a)). When the cilia spacing is large ($a/L = 5$ and 2.5), the flow generated remains approximately constant for all metachronal wave speeds. The increase in flow by decreasing the cilia spacing from $a/L = 5$ to $a/L = 2.5$ is much larger when the cilia beat out-of-phase compared to the increase when the cilia beat in-phase. However, when the cilia spacing is low
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Figure 7.5: (a)-(d) Snapshots for the out-of-phase motion of cilia between time instances of Figs. 7.4(b) and 7.4(c) for $\Delta \phi = \pi/6$ ($n = 12$) with the wave moving to the right (antiplectic metachrony) for $a/L = 1.67$. The contours represent the absolute velocity normalised with $L/t_{\text{beat}}$. The direction of the velocity is represented by streamlines. The white circles represent fluid particles. The applied magnetic field at each cilium is represented by the white arrows.

(e) Instantaneous flux (right axis) and flow (left axis) as a function of time with the instances (a)-(d) duly marked.

For $a/L = 1.67$, we see a larger increase in the fluid flow when there is an antiplectic metachrony (AM) compared to a symplectic metachrony (SM). Also, the effectiveness sharply increases from around 0.3 (i.e., 30% of the totally displaced fluid is converted into net flow) to 1 (fully unidirectional flow), see Fig. 7.7(b). To analyse these trends a bit further, we plot the positive and negative flow ($Q_p$ and $Q_n$ in Fig. 7.1) created during a beat cycle for different phase differences in Fig. 7.8(a). It can be seen that the cilia do not create a negative flow when they beat out-of-phase for all cilia spacings, resulting in a unidirectional flow (effectiveness = 1). This reduction in negative flow is due to the shielding of flow during the recovery stroke caused by the effective flow of other cilia. It can also be noted that the positive flow is also reduced compared to in-phase beating, but the reduction is considerably less than the reduction in negative flow. Thus, the net flow increases as soon as the cilium start to beat out-of-phase (see Fig. 7.7(a)). It can be seen from Fig. 7.8(a) that in the presence of metachronal waves when the cilia spacing is large ($a/L$ = 5), the fluid transported during the effective stroke remains nearly the same for all values of the wave velocities. For small cilia spacing ($a/L = 1.67$), however, the positive flow is maximal for antiplectic metachrony, which leads to a larger net flow...
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Figure 7.6: (a) Normalised fluid flux as a function of time for $a/L = 1.67$ and different values of phase difference $\Delta\phi$. (b) Normalised accumulated flow at any time $t$ during the beat cycle.

Figure 7.7: Flow and effectiveness as a function of the phase difference $\Delta\phi$ for different inter-cilium spacings $a/L$. AM and SM refer to antiplectic metachrony (the wave direction is opposite to the direction of the effective stroke) and symplectic metachrony (the wave direction and the effective stroke direction are the same), respectively.

For antiplectic metachrony compared to symplectic metachrony.

To understand the difference in positive flow for opposite wave directions for small inter-cilium spacing ($a/L = 1.67$), we plot the flux as a function of time scaled with the time taken by the magnetic couple to travel from one cilium to the next $t_1$, for two different metachronal wave velocities ($3/t_\text{beat}$ and $6/t_\text{beat}$ cilia per second), see Fig. 7.8(b). The corresponding phase differences are also shown in the legend. It can be seen that the flux in the case of antiplectic metachrony is larger than the flux created by the symplectic metachrony for the same wave speed. This difference in flux for opposite wave directions can be understood by analysing the velocity field corresponding to symplectic and antiplectic metachrony at time instances when the flux is maximum (see Fig. 7.9). Figure 7.9(a) and 7.9(b) correspond to different phase differences ($\Delta\phi = \pi/6$ and $\Delta\phi =$ \[
\frac{\pi}{6}\).
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Effect of metachronal waves

Phase difference $\Delta \phi$ in units of $\pi$

Flow per cycle/$\pi L^2/2$

- $a = 5L$
- $a = 2.5L$
- $a = 1.67L$

Positive flow ($Q_p$)
Negative flow ($Q_n$)

AM SM

(a)

Figure 7.8: (a) Positive ($Q_p$) and negative flow ($Q_n$) (see Fig. 7.1) created by the cilia corresponding to the results presented in Fig. 7.7. (b) Flux vs time (scaled with the time $t_1$ taken by the magnetic couple to travel from one cilium to the next) for $a/L = 1.67$ and different wave speeds.

5$\pi/6$, respectively) leading to a similar wave speed of $6/t_{beat}$ cilia per second (see also Fig. 7.2). The fifth cilium is in the peak of its effective stroke for both AM and SM. In the case of symplectic metachrony, the positive flow created by the fifth cilium is obstructed by the close proximity of the fourth cilium, which has just started its effective stroke. As a result, we observe the formation of a vortex. In the case of antiplectic metachrony, however, the position of the fourth cilium is such that the positive flow created by the fifth cilium is not obstructed. This leads to larger fluid flow in the positive direction, so that the net flow created by an antiplectic metachrony is larger than that created by its symplectic counterpart.

Reports on metachrony and phase locking of beating cilia have appeared in the past (Gauger et al., 2009; Kim & Netz, 2006; Gueron et al., 1997; Gueron & Levit-Gurevich, 1999). The main results are that metachrony enhances flow compared to synchronously beating cilia (Kim & Netz, 2006; Gauger et al., 2009) and that antiplectic metachrony generates a higher flow rate than symplectic metachrony (Gauger et al., 2009). (Kim & Netz, 2006) analysed two cilia, which are driven by internal motors and are moving out-of-phase due to the hydrodynamic interaction. They have shown that the fluid propulsion increases, once the cilia start to beat with a phase difference, which is in agreement with our results. Our results also agree with (Gauger et al., 2009), where it is shown that the fluid flow is larger in the case of antiplectic metachrony than symplectic metachrony when the cilia are close together. However, our results differ from (Gauger et al., 2009) in the sense that we always see an enhancement in flow in the presence of metachrony (compared to cilia beating in-phase) irrespective of the direction and magnitude of the metachronal wave velocity. This is most likely due to the fact that the asymmetry in ciliary motion in our case is much higher. (Gueron et al., 1997) and (Gueron & Levit-Gurevich, 1999) have proposed that the evolution of the out-of-phase motion of cilia in Paramecia is due to hydrodynamic interactions between adjacent cilia leading to antiplectic metachrony. It is interesting to observe that the interplay between the internally-driven actuation and hydrodynamic interaction in nature results in antiplectic
Figure 7.9: (Colour online) Snapshots for antiplectic ($\Delta\phi = \pi/6$) and symplectic metachrony ($\Delta\phi = 5\pi/6$) for a wave speed of $6/t_{\text{beat}}$ cilia per second and cilia spacing $a/L = 1.67$ at $t = 0.1t_1$ of Fig. 7.8(b). The contours represent the absolute velocity normalised with $L/t_{\text{beat}}$ (blue and red colours represent a normalised velocity of 0 and 2, respectively). The direction of the velocity is represented by streamlines. The applied magnetic field is shown by the white arrows.

metachrony. Our results, and those of others (Gauger et al., 2009), show that indeed antiplectic metachrony leads to larger flow than symplectic metachrony for small cilia spacings as typically seen in nature.

7.2.2 Out-of-phase motion caused by a non-uniform magnetic field

Problem statement

We now study the flow generated by magnetic artificial cilia, which are actuated using a rotating and non-uniform magnetic field ($\mathbf{B}_0 = (B_{x0}, B_{y0})$) that varies in space and time:

$$B_{x0} = B_0 \cos(\omega t \pm 2\pi x/\lambda), \quad B_{y0} = B_0 \sin(\omega t \pm 2\pi x/\lambda), \quad (7.2)$$

where $B_0$ is the magnitude of the applied magnetic field, $\lambda$ the wavelength of the non-uniform magnetic field, $\omega = 2\pi/t_{\text{ref}}$ is the angular frequency and $t_{\text{ref}}$ is the time period of the magnetic field, see Fig. 7.10. The applied magnetic field travels in space and time with a velocity $\lambda/t_{\text{ref}}$, which is positive (i.e., to the right) when a negative sign is used in Eqn. 7.2, and negative when a positive sign is used.

In addition to the body couple $\mathbf{M} \times \mathbf{B}_0$ (analysed in sections 2.3 and 5.2.1), the non-uniform magnetic field causes a magnetic body force of magnitude $\mathbf{M} \cdot \nabla \mathbf{B}_0$ to act on the cilia, where $\mathbf{M} = (M_x, M_y)$ is the magnetization of the cilia. Its components in the $x$ and $y$ directions are $M_x B_{x0,x}$ and $M_y B_{y0,x}$, respectively. Since the magnetization $M_x$ scales with $B_{x0}$, the magnetic body forces in the $x$ and $y$-direction scale as $\mp \sin 2\theta/\lambda$ and $\pm \cos^2 \theta/\lambda = \pm (1 + \cos 2\theta)/2\lambda$, respectively, where $\theta = \omega t \pm 2\pi x/\lambda$; the top and bottom signs are used for a negative and positive wave velocity, respectively. It is to be noted that the magnetic body forces scale with $2\theta$. From Eqn. 2.37, it can be seen that
The magnetic body force also scales with $2\theta$. Thus, the frequency of the magnetic body forces and body couple is $\omega_M = 2\pi/l_{\text{beat}} = 2\omega$ and their wavelength is $\lambda_M = \lambda/2$. As mentioned earlier, this causes two ciliary beats in one period of rotation of the magnetic field, and two cilia spaced $\lambda_M$ apart beat identically. It is important to note that the magnetic body force in the $y$-direction is positive (or negative) for the magnetic waves travelling to the left (or right). In addition, the magnetic body forces decrease when the wavelength is increased and converges to zero when a uniform field ($\lambda \to \infty$) is applied as in previous section.

As the wavelength of the magnetic forces (both body couple and body forces) is $\lambda_M$, the cilia beat in-phase when $a = \lambda_M$ and $a < \lambda_M$ and in anti-phase when $a = \lambda_M/2$. When $0 < a < \lambda_M/2$, the magnetic field causes a metachronal wave whose direction coincides with the direction of the magnetic wave; when $\lambda_M/2 < a < \lambda_M$ the metachronal wave is opposite to the direction of the magnetic wave (Khaderi et al., 2011b). The metachronal wave is named symplectic, SM (or antiplectic, AM) when the metachronal wave travels in the same (or opposite) direction as the effective stroke.

We perform the simulations in the Stokes limit with the fluid, magnetic and inertia numbers set to 0.15, 10.89 and $4.8 \times 10^{-3}$, respectively. The values of the dimensionless parameters correspond to $L = 100$ microns, $E = 1$ MPa, the thickness of cilia linearly decreased from $h = 2$ $\mu$m at the fixed end to 1 $\mu$m at the free end, $\rho_f = 0.1$ kg/m$^3$, $\mu = 1$ mPas, $\rho = 1000$ kg/m$^3$, $B_0 = 18.8$ mT and the cycle time $t_{\text{ref}} = 2t_{\text{beat}} = 20$ms. The magnetic susceptibilities of the cilia are 4.6 along the length and 0.8 along the thickness (van Rijsewijk, 2006).

### Analysis of cilia deformation

The travelling magnetic field leads to a distribution of magnetic couples which is significantly different from the couples in case of a uniform magnetic field. In Fig. 7.11, we neglect the body forces and plot the area swept by the tip of the cilia as a function of $L/\lambda_M$ for various cilia spacings. For reason shown later, we limit ourself to the cases where the cilia spacing $a < \lambda_M/2$. While performing simulations, we apply the magnetic field in Eqn. 7.2 with positive and negative signs for symplectic and antiplectic metachrony, respectively. The top axis of Fig. 7.11 corresponds to symplectic metachrony, and the bottom axis to antiplectic metachrony. It can be seen that the swept area for the sym-
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plectic metachrony is significantly larger compared to synchronously beating cilia (see Fig. 7.11), while the opposite is the case for antiplectic metachrony. This is due to the fact that the cilia are exposed to the system of magnetic couples for longer (shorter) duration of time for SM (AM) compared to synchronously beating cilia, causing an increased (decreased) swept area.

We now analyse the influence of the magnetic body forces on the asymmetry of the ciliary motion for symplectic and antiplectic metachrony. For illustrative purposes, we choose the case of $a = 5L$ and $L/\lambda_M = 0.1$ to plot the motion of a cilium at different time instances after a steady state has been reached (see table 7.1). The thick arrows, hollow arrow heads and thin arrows represent the applied magnetic field, magnetization and magnetic body forces, respectively. Also shown are the signs of the magnetization in the $x$-direction, field gradients and body forces. As the magnetic field vector at any point rotates counterclockwise irrespective of the travel direction of the wave, the resulting field distribution in space depends on the travel direction. It can be seen that the direction of the magnetization strongly correlates with the direction of the applied magnetic field. The magnetization in the $x$-direction is maximum during the recovery stroke and initial part of the effective stroke, see the instances (a), (b), (g) and (h) in table 7.1, when the field vector makes an angle $0$ or $\pi$ with the $x$ axis. During these instances $B_{x0,x} \rightarrow 0$ and $B_{y0,x}$ is maximum, leading to magnitudes of the body forces that are larger compared to other instances during the beat cycle. It can be seen that the body forces (red arrows in table 7.1) act such that they make the film stay closer to (or further away from) the substrate in the case of antiplectic (or symplectic) metachrony. Therefore, the cilia stay closer to the bottom boundary for antiplectic metachrony, which results in a larger area swept and fluid flow than symplectic metachrony (shown later). The magnetic body forces and body couples complement each other during the beginning of the effective stroke in the case of symplectic metachrony. However, for antiplectic metachrony they oppose each other. As a result, for small wavelengths the magnetic body forces will be very large and do not allow the cilia to beat. The non-uniform magnetic field thus influences the motion of the cilia in two ways: the magnetic body forces (which decrease

**Figure 7.11**: Area swept by the cilia as a function of $L/\lambda_M$ for different $a/L$ under the sole influence of magnetic body couples caused by a travelling non-uniform magnetic field.
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Area swept as a function of $L/\lambda$ for different inter-cilium spacings $a/L$ under the influence of magnetic couples as well as forces.

The area swept by the cilia under the influence of both body forces and couples as a function of $L/\lambda_M$ for different cilia spacings is shown in Fig. 7.12. By comparing Fig. 7.11 with Fig. 7.12, it can be clearly deduced that the effect of body forces dominated over the effect of body couples, leading to a larger swept area for AM compared to SM. As mentioned earlier (see table 7.1), for small wavelengths ($\lambda_M < 0.15L$) the body forces acting towards the bottom boundary in the case of AM are so high that the area swept by the cilia diminishes and in some cases the cilia do not beat at all.

Analysis of fluid flow

Next, we analyse the flow created by the metachrony. We first focus on antiplectic metachrony (the wave moving to the right) for a wavelength $\lambda_M = 6a$ and cilia spacing $a = 1.67L$. The deformed position of the cilia at different time instances in addition to the fluid pressure profiles is shown in Fig. 7.13. The contours represent the pressure in the fluid, the direction of the fluid velocity is shown using the streamlines, the magnetic field distribution is given by the black arrows and the white circles represent the fluid particles. In Fig. 7.13(a) cilium 1 is performing the recovery, in Fig. 7.13(b) cilium 2 is performing the recovery, and so on, clearly showing that the magnetic wave is travelling to the right. It can be seen that the flow and pressure profiles are similar after every $t_{beat}/6$ seconds, but have translated in the direction of the metachronal wave by one cilium. Let us focus our attention on instance $t = 2t_{beat}/6$ (Fig. 7.13(b)). The first cilium has just finished its beat cycle and the second cilium is performing the recovery stroke, while the remaining four cilia are in different phases of their effective stroke. Due to the out-of-phase motion of the cilia, the pressure to the right of cilium 2 is much larger than to its left. In this situation the recovery stroke of the cilium 2, instead of creating a negative flow, creates a local vortex. As a result, the negative flux and flow are drastically knocked down, leading to a substantial increase of the net fluid propelled.
Consequently, the created fluid flow is unidirectional. This can also be seen from the variation of the flux and flow as a function of time (see Fig. 7.13(h)). The six periodic dips in the flux profile are caused by the recovery stroke of the cilia. The negative flux, however, is very small compared to the positive flux, which leads to a nearly monotonous increase of the fluid flow with time and a much larger fluid flow at the end of a cycle (0.6 in units of \(\pi L^2/2\)) compared to the synchronously moving cilia (0.2 in units of \(\pi L^2/2\), see Fig. 5.4).

The flow (normalised by \(\pi L^2/2\)) and effectiveness are plotted as a function of \(L/\lambda_M\) for different cilia spacings in Fig. 7.14. For a given cilia spacing, the flow nicely correlates with the area swept by the free end of the cilia (compare Figs. 7.12 and 7.14(a)). This was also observed in our earlier studies (Khaderi et al., 2009, 2010) for the case of uniformly beating cilia. In the case of symplectic metachrony, as the wavelength gets smaller the magnetic body forces increase, pushing the cilia away from the bottom boundary, which causes a larger negative flow (see the dashed lines in Fig. 7.14(c) for symplectic metachrony), and a resulting decrease in the net fluid transported and effectiveness. At small wavelengths (\(\lambda_M < 4L\)) of antiplectic metachrony, the magnetic body forces acting during the beginning of the effective stroke are large and do not allow the cilia to exhibit a complete effective stroke. Now, the positive flow is low (see the solid lines in Fig. 7.14(c) for antiplectic metachrony), causing the net fluid transported and effectiveness to attain low values.

In most of the cases, the flow caused by the metachronal motion of the cilia is larger than that of the synchronously beating cilia, even though the area swept in the latter case is larger. This, as seen earlier, is because of the reduction in the negative flow caused by the recovery-induced vortex formation (see also (Khaderi et al., 2011b)). In fact, as shown in Fig. 7.14(c), the positive flow is also reduced. However, the reduction in the negative flow is more than the reduction in the positive flow. Consequently, the effectiveness of fluid propulsion is also higher compared to synchronously beating cilia (see Fig. 7.14(b)). When the cilia spacing is decreased the viscous resistance per cilium decreases, which causes the normalised flow to increase. However, decreasing the cilia spacing below \(2.5L\) does not increase the fluid propelled for symplectic metachrony. In these cases, the cilia are close together during their effective stroke, which leads to an obstruction of the positive flow of a cilium by its neighbours (Khaderi et al., 2011b).

It can thus be seen that in the presence of non-uniform magnetic fields we obtain a significant enhancement in the fluid flow for the case of antiplectic metachrony. However in the case of symplectic metachrony, the increase in the flow is only limited.

### 7.3 Conclusions

We have studied the flow created by a two-dimensional array of artificial cilia as a function of the phase lag and spacing between neighbouring cilia. Two methods of generating a metachronal wave are considered; by prescribing a phase difference between adjacent cilia and by using a non-uniform magnetic field. In the latter case, the magnetic body forces acting on the cilia lead to a reduction of the asymmetric area for the case of symplectic metachrony compared to antiplectic metachrony. The flow per cycle and the effectiveness (which is a measure of the unidirectionality of flow) are considerably enhanced when the cilia start beating out-of-phase, as compared to synchronously beating cilia. While the amount of flow enhancement depends on the inter-cilia spacing, the effectiveness is not
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Figure 7.13: (a) - (f) Contours of pressure normalised with $\mu/t_{\text{beat}}$ at different time instances. The direction of the fluid flow is represented by the streamlines, the magnetic field distribution is shown using the black arrows and the white circles represent fluid particles. (h) Flow and flux as a function of time, with the instances corresponding to (a) - (f) duly marked.

significantly influenced. Metachrony is observed to completely knock-down the negative flow to zero due to the vortex formation caused by the shielding of the recovery stroke. Interestingly, we find that the enhancement is achieved even for small phase differences and large wavelengths. In the case of metachronal waves obtained by prescribing a phase difference, the direction of travel of the metachronal wave is not important for large cilia spacings. In all other cases, the fluid flow is larger for antiplectic metachrony
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Figure 7.14: Flow and effectiveness as a function of $a/\lambda$ for different inter-cilium spacings $a/L$. AM and SM refer to antiplectic metachrony (the wave direction is opposite to the direction of the effective stroke) and symplectic metachrony (the wave direction and the effective stroke direction are the same), respectively. The area flow is significantly enhanced for an antiplectic metachrony compared to symplectic metachrony.

compared to symplectic metachrony, which is related to the obstruction of the positive flow for symplectic metachrony. It is therefore beneficial if the magnetic actuation of the artificial cilia is designed such that it results in an antiplectic metachrony. Our results suggest that an antiplectic metachrony is adopted by the cilia on paramecia and in the respiratory system to maximize the fluid propelled. However, ciliary systems (such as on Opalina) that exhibit symplectic metachrony are also present in nature. It will be of interest to investigate what property is optimised by symplectic metachrony in these systems.
Table 7.1: Motion of a super-paramagnetic cilium under the influence of a non-uniform rotating magnetic field that travels in space to the left (symplectic metachrony) and right (antiplectic metachrony). The thick arrows, hollow arrow heads and thin arrows represent the applied magnetic field, magnetization and magnetic body forces, respectively. The direction of the magnetization ($M_z$), field gradients ($B_{x,x}$ and $B_{y,x}$) and body forces ($f_x$ and $f_y$) at different instants are also shown using the + and - symbols.