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Perceptual basis of bimanual coordination

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Periodic bimanual movements are often the focus of studies of the basic organizational principles of human actions[1–25]. In such movements there is a typical spontaneous tendency towards mirror symmetry. Even involuntary slips from asymmetrical movement patterns into symmetry occur, but not vice versa. Traditionally, this phenomenon has been interpreted as a tendency towards co-activation of homologous muscles, probably originating in motoric neuronal structures. Here we provide evidence contrary to this widespread assumption. We show for two prominent experimental models—bimanual finger oscillation[1] and bimanual four-finger tapping[2]—that the symmetry bias is actually towards spatial, perceptual symmetry, without regard to the muscles involved. We suggest that spontaneous coordination phenomena of this kind are purely perceptual in nature. In the case of a bimanual circling model, our findings reveal that highly complex, even 'impossible' movements can easily be performed with only simple visual feedback. A 'motoric' representation of the performed perceptual oscillation patterns is not necessary. Thus there is no need to translate such a 'motoric' into a 'perceptual' representation or vice versa, using 'internal models' (ref. 29). We suggest that voluntary movements are organized by way of a representation of the perceptual goals, whereas the corresponding motor activity, of sometimes high complexity, is spontaneously and flexibly tuned in.

How do coordinative processes in the motor system and in the domain of perception and imagery contribute to the organization of voluntary movement? Spontaneous coordination phenomena such as the symmetry tendency in bimanual movements are of particular interest here. The traditional view is that the symmetry tendency is due to a bias towards co-activation of homologous muscles[1,3], probably originating in motoric neuronal structures. Recently, the possible influence of perception and perceptual imagery on spontaneous coordination phenomena has been stressed[4–8,26]. However, many of these studies tend to assume that motoric, or efferent, constraints are also of central importance. Clear experimental evidence is lacking.

In our first experiment we addressed the symmetry tendency in a classical bimanual finger oscillation model[1,2,9,10]: a person stretches out both index fingers and oscillates them in mirror symmetry or in parallel (Fig. 1a, b). The symmetrical mode is much more stable than the parallel mode. With increasing oscillation frequencies, a parallel pattern often involuntarily switches into a mirror-symmetrical movement pattern. In contrast, symmetrical movements never switch into asymmetry. Is this symmetry bias

towards co-activation of homologous muscles or towards perceptual, spatial symmetry?

Participants ($n = 8$) performed bimanual index-finger oscillations, either in symmetry or in parallel, with both movement instructions (symmetry or parallelity) defined in visual, perceptual space. To register trajectory, both fingers were inserted in cuffs of 50-g weight, with a graphics tablet stylus attached to each finger. The hands were individually put either palm up or palm down. Thus, there were four bimanual hand positions (Fig. 1c–f). If both palms are either up or down, the hand position is congruous. If one palm is up and the other is down the hand position is incongruous. In a session, each combination of movement instruction and hand position was performed four times, in a total of 32 randomized trials. In a trial, a metronome pulse paced the oscillation frequency from 1.4 Hz up to 3.6 Hz, in a time interval of 24 s. Participants were requested to execute one full movement cycle on each beat. Should the movement pattern change, participants were instructed to give in and perform the more comfortable pattern[11].

The experimental rationale, as adopted from designs in the literature[7,12–14], was as follows. With a congruous hand position, perceptual movement symmetry goes along with periodic co-activation of homologous muscles. Thus, a bias towards symmetrical oscillation is to be expected, as it is a replication of results reported previously. The critical condition is with incongruous hand position, because perceptual parallelity goes along with co-activation of homologous muscles. Thus, if there is a dominant tendency towards co-activation of homologous muscles, a bias towards parallel oscillation is to be expected. If there is a dominant tendency towards perceptual symmetry, there should be a bias towards symmetrical oscillation.

The results were clear: independent of hand position, an instructed symmetrical oscillation pattern is always stable, whereas instructed parallel oscillations tend to disintegrate and to switch into symmetry. Figure 2 demonstrates this by showing histograms of the relative phase of the fingertips, as defined in a position versus velocity coordinate system[11,15]. Zero degrees relative phase means symmetry, whereas 180° relative phase means parallelity, in perceptual space. Relative phase was calculated on every right reversal of the left finger.

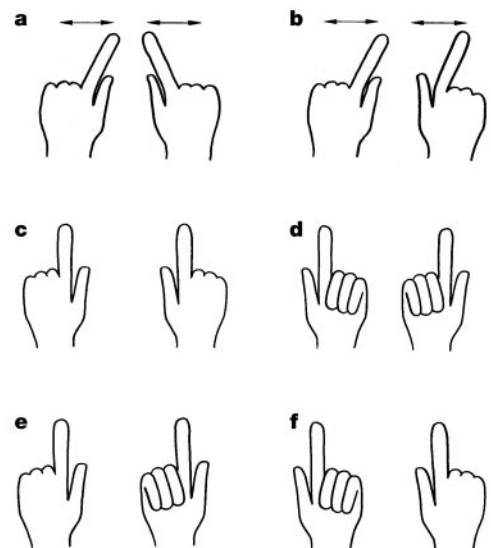We define a relative phase of $0 \pm 60°$ as symmetry, of $180 \pm 60°$ as

Figure 1 Instructed, synchronous finger oscillation patterns and hand positions.
a, Symmetrical movement. **b**, Parallel movement. **c**, **d**, Congruous positions with both palms up or both palms down. **e**, **f**, Incongruous positions with one palm up and the other palm down.

parallelity and of $90 \pm 30°$ or $270 \pm 30°$ as an intermediate mode[16]. The distribution of these modes was calculated for the last 4 s in each trial. With the incongruous hand positions, the proportion of other modes than the instructed one was significantly higher under an instruction of parallelity (59.17%) than under symmetry instruction (9.70%) ($P < 0.001$, paired t-test). With the incongruous hand positions and parallelity instruction, symmetry was the most frequent coordination mode among the non-instructed modes (symmetry, 46.38%; intermediate, 12.79%, $P < 0.001$). With the incongruous hand positions and symmetry instruction, there were virtually no transitions into parallelity (parallelity, 0.75%). This general pattern of results does not change when a view of the fingers is prevented and participants have to rely solely on proprioception (data not shown).

We conclude that the symmetry tendency in the bimanual finger oscillation model is a tendency towards perceptual, spatial symmetry, rather than towards co-activation of homologous muscles.

This is a challenging result. The idea that constraints in the motor system might bring about the symmetry tendency has been based on the assumption that there is a general tendency towards co-activation of homologous muscles. Theorists proposed, for example, that mechanisms such as bilateral cross-talk in motoric neuronal structures might cause this tendency[17]. Or there might be a mechanism that eases motor programming by taking advantage of homologies[18]. If it turns out that there is no general tendency towards co-activation of homologous muscles, the very existence of such motoric constraints may also seriously be doubted.

In our second experiment we addressed the symmetry tendency in a bimanual finger-tapping model[2]. A person stretches out the index (I) and middle (M) fingers of both hands and taps on the table with the fingertips. We denote this finger combination by (MI·IM). Symmetrical tapping is defined as synchronous tapping of both index fingers in periodic alternation to synchronous tapping of both middle fingers, that is (_I·I_), (M_·_M), (_I·I_), and so on. Parallel tapping means synchronous tapping of the left middle and the right index finger in periodic alternation to synchronous tapping of the left index and the right middle finger: (M_·I_), (_I·_M), and so on. In parallel tapping, the movement pattern is less stable than in symmetrical tapping. Involuntary transitions into symmetry occur with higher tapping frequencies. Is this symmetry bias towards co-activation of homologous muscles, and thus possibly motoric in nature, or towards perceptual, spatial symmetry?

Participants ($n = 10$) were instructed to perform symmetrical as well as parallel bimanual tapping patterns using four fingers. For
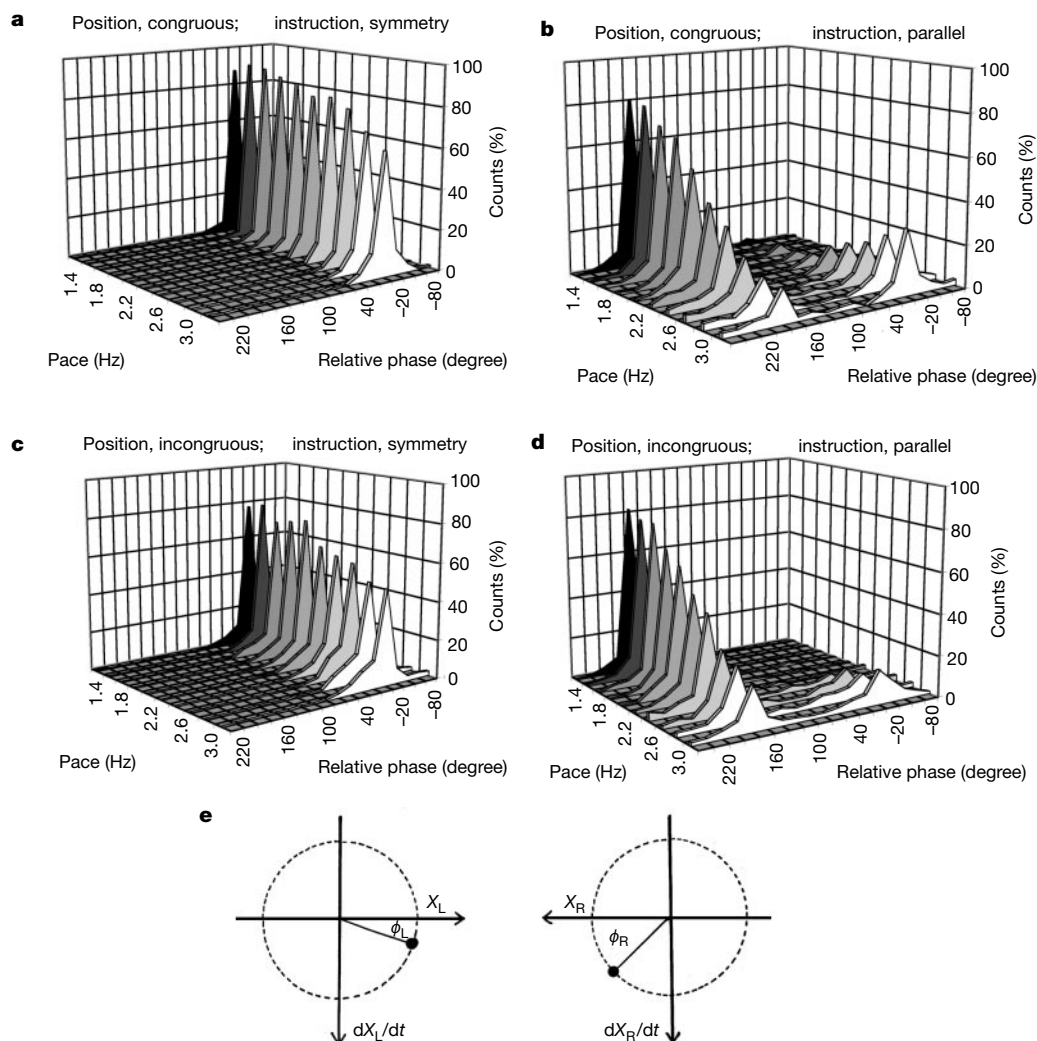

Figure 2 Relative phase of the fingertips averaged across subjects in experiment 1. **a**, Congruous hand positions and symmetrical movement instruction. **b**, Congruous hand positions and parallel movement instruction. **c**, Incongruous hand positions and symmetrical movement instruction. **d**, Incongruous hand positions and parallel movement instruction. **e**, Coordinate systems as used for defining relative phase, Θ (ref. 15). X_R and X_L indicate the transversal positions of the right and left index finger, respectively; dX_R/dt and dX_L/dt their velocities. $\Theta = \varphi_R - \varphi_L = \tan^{-1}[(dX_R/dt)/X_R] - \tan^{-1}[(dX_L/dt)/X_L]$.

registration of the onset time of the taps, the fingers tapped on four small metal plates, which were connected to a computer. The acting fingers of an individual hand were either the index and middle finger, or the middle and ring finger. Thus, there were four bimanual finger settings. If the finger combinations of both hands are identical, the finger setting is called congruous, otherwise the finger setting is incongruous. For example, symmetrical tapping in an (MI·MR) finger setting means (_I·M_), (M_·_R), (_I·M_),… In a session, each combination of movement instruction and finger setting was performed four times, in a total of 32 randomized trials. In a trial, a metronome pulse paced the tapping frequency from 1 Hz up to 3 Hz, in a time interval of 45 s. Participants were requested to execute one full movement cycle on each beat. Should the movement pattern change, participants were instructed to give in and perform the more comfortable pattern.

The experimental rationale was analogous to that of experiment 1: with a congruous finger setting, perceptual movement symmetry goes along with periodic co-activation of homologous fingers and muscles. Thus a bias towards symmetry is to be expected, as it is a replication of results reported previously. The critical condition is, again, the incongruous setting. In this case, homologous fingers are co-active only in the parallel pattern. In the case of a tendency towards co-activation of homologous muscles, the parallel pattern should be the more stable one. In the case of a bias towards perceptual symmetry, the symmetrical pattern should be of greater stability.

The results were, again, clear. Independent of the finger setting, an instructed symmetrical pattern was always stable whereas parallel patterns heavily switched into symmetry with increasing tapping frequencies. Figure 3 demonstrates this by displaying the percentage of symmetrical taps for congruous and incongruous finger settings, under both instructions.

Where one finger of the right hand and one finger of the left hand tap together in a time window of 70 ms, this event is categorized as a synchronous tap. Each synchronous tap can individually be categorized as symmetrical or parallel. Symmetrical and parallel taps were counted separately. For analysis, each trial was separated into four intervals of equal length, 5–15 s (mean frequency 1.1 Hz), 15–25 s (1.4 Hz), 25–35 s (1.9 Hz) and 35–45 s (2.9 Hz). To statistically confirm the reported results the data were entered into a $2 \times 2 \times 4$ repeated-measurements analysis of variance; the factors were instruction, finger setting, and time interval. An α-level of 0.01 was always applied. The analysis revealed highly significant main effects for instruction ($F_{1,9} = 30$) and for interval ($F_{3,27} = 14$), as well as a highly significant interaction between these two factors ($F_{3,27} = 16$). The main effect for congruency and the remaining interactions were not significant. This general pattern of results does not change

when the fingers cannot be seen and participants have to rely solely on proprioception (data not shown).

We conclude that the symmetry tendency in the investigated model of four-finger tapping is not a tendency towards co-activation of homologous muscles, but instead arises in the functional domain of perception and perceptual imagery.

Observations on further bimanual oscillation models confirm the obtained results. There is obviously no general tendency towards co-activation of homologous muscles. Therefore, motoric interpretations of the symmetry tendency are no longer plausible. Instead, the hypothesis that the symmetry tendency in bimanual oscillation is purely perceptual in nature seems justified.

We speculate that perception and imagery provide a plausible, unifying explanatory principle, not only for the symmetry tendency, but also for other spontaneous bimanual coordination phenomena of a similar kind.

In experiments 1 and 2, the perceptual oscillation pattern—that is, symmetry or parallelity (antiphase)—could always be predicted from the bimanual muscle activation pattern. This includes the possibility that the central nervous system might bring about the intended movement pattern by way of activating a corresponding motoric pattern. It is a common assumption in theories concerning human motor control that voluntary movement performance relies on a translation of a characteristic, corresponding motoric pattern into the intended sensory pattern, and vice versa[27–29]. In our next experiment we investigated whether the existence of such characteristic, corresponding motoric patterns is necessary for symmetrical and antiphase bimanual circling.

In our third experiment we addressed a bimanual circling model, as introduced previously (refs 19, 20). When humans circle both hands in a horizontal plane, only a few synchronous circling patterns are stable. There is a tendency towards synchronization and, in particular, symmetry. Especially difficult, and almost impossible for untrained persons, are circling patterns under non-harmonic frequency ratios of the hands, such as a 5:4 or 4:3 frequency ratio.

Right-handed participants ($n = 8$) circled two visible flags, by way of two cranks that were hidden under the table (Fig. 4a). The left flag circled directly above the left crank and hand, whereas the right flag circled in a 4:3 frequency ratio to the right crank and hand, owing to a gear system. Thus, iso-frequency in the flags went together with a 4:3 frequency ratio in the cranks (hands). Movements were registered by way of a graphics stylus tablet inserted in each crank.

The participants either circled both flags (hand agency), or circled the right flag alone, while a motor driven by the experimenter (motor agency) circled the left flag. Participants were instructed to
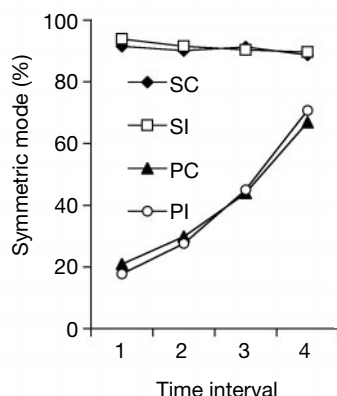

Figure 3 Percentage of symmetrical taps, in experiment 2, split by movement instruction and bimanual finger setting (see text). SC, instruction is symmetry; finger setting is congruous. SI, symmetry; incongruous. PC, parallelity; congruous. PI, parallelity; incongruous.
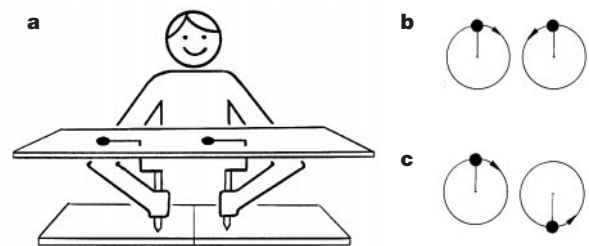

Figure 4 Apparatus used in experiment 3, and instructed synchronous circling patterns of the flags. **a**, Apparatus. The participant circles two visible flags using his or her hidden hands. The left flag moves coincidentally with the left hand whereas the right flag moves according to a well defined angle and/or frequency transformation with regard to the right hand (see text). **b**, Symmetry, that is, 0° relative angle. **c**, Antiphase, that is, 180° relative angle. Relative angle is defined in analogy to relative phase as described in Fig. 2e, this time in Y versus X position coordinate systems instead of dX/dt versus X.
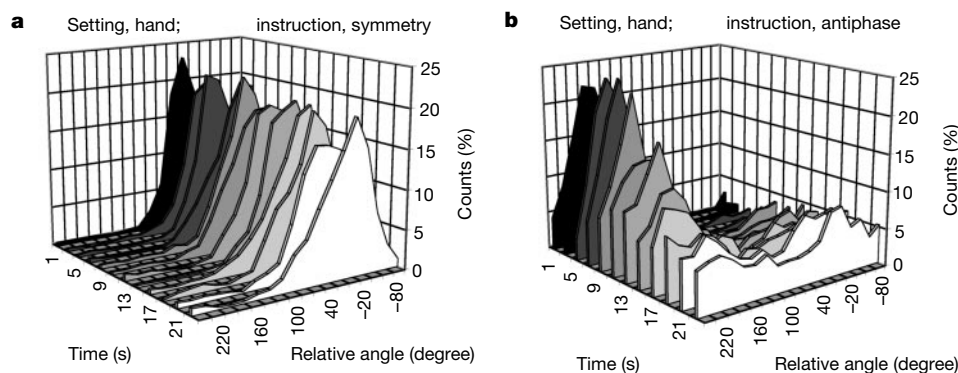
Figure 5 Histograms of relative angle of the circling flags, averaged across subjects in experiment 3. The right flag circled in a 4:3 frequency ratio to the right hand (see text). **a**, Hand agency and symmetry movement instruction. **b**, Hand agency and antiphase movement instruction.

circle the flags inwards and maintain the visual circling pattern either in mirror symmetry (0° relative angle, see Fig. 4b) or in antiphase (180° relative angle, see Fig. 4c). In a trial of 30-s duration, participants began at a slow, comfortable velocity and then speeded up to a velocity they considered fast, but not beyond the point they lost visual control. Before the experiment, participants were told that in situations where they felt a tendency towards a circling mode other than instructed, they should give in and maintain the preferred mode. After a 15–20 min training period, each participant performed 40 experimental trials, in a blocked 2 agency × 2 movement instruction design, which was balanced across subjects.

The main rationale was as follows. First, owing to the frequency transformation in the right hand and flag system, symmetry or antiphase in the flags cannot be predicted from the corresponding hand movement pattern, which is identical in both cases. Second, performing bimanual oscillations in a 4:3 frequency ratio is practically impossible for naive subjects as an explicit task[2]. This was confirmed by a control experiment that was adapted to our model. In consequence, no body-oriented strategy is possible to bring about iso-frequency in the flags, let alone symmetry or antiphase. If participants were able to perform any of the instructed movement patterns, this would certainly be solely due to visual strategies. It would be of additional interest whether manifest transitions from antiphase into symmetry occur in the flags, as such a tendency is certainly perceptual in nature.

All participants were able to circle the flags in symmetry and speed up, under both hand and motor agency. Antiphase was also manageable but was corrupted with increasing circling velocities. In addition, switches into symmetry occurred. Figure 5 demonstrates this by showing histograms of the relative angle of the flags. A relative angle of 0° means symmetry, whereas 180° means antiphase. Relative angle was calculated on every right reversal of the left flag.

We defined coordination modes in analogy to the procedure reported for experiment 1, and calculated their distribution for the last 4 s of the trials. In the last 4 s, under both agencies, the proportion of modes in the flags other than the instructed one was significantly higher under antiphase instruction than under symmetry instruction (hand agency, 65.38% versus 21.03%, respectively; motor agency, 71.31% versus 13.44%, respectively, in both cases, $P < 0.001$). Under antiphase instruction, symmetry tends to be the most frequent coordination mode among the non-instructed modes (hand agency: symmetry, 38.61%; intermediate, 26.77%, $P = 0.076$; motor agency: symmetry, 50.79%; intermediate, 20.52%, $P < 0.001$). A certain symmetry tendency with regard to the hidden hands was also revealed, but solely under hand agency and symmetry instruction. Anecdotal evidence seems to suggest that attention to the hands disrupts control of iso-frequency in the flags.

We conclude that symmetry and antiphase in the flags can be achieved in visual space even though there is no specific translation of characteristic body activity patterns into these characteristic perceptual patterns. To bring about the instructed flag movements, participants easily perform otherwise impossible body movements. Finally, a tendency to circle the flags in symmetry, independent of what the hands are doing, supports the notion that the symmetry tendency in the bimanual circling model is purely perceptual in nature.

Taken together, our results provide evidence that bimanual coordination is much more independent of coordinative processes in the motor system than is often thought. The symmetry tendency in bimanual movements is independent of muscular and motoric constraints and is thus purely perceptual in nature. A perceptual interpretation seems to hold also for other spontaneous coordination phenomena of the same kind. In our last experiment, not only spontaneous but also intentional symmetry and antiphase are clearly organized exclusively in the domain of perception and perceptual imagery. There is no need of a representational counterpart in the motor system and thus, trivially, no need of its translation using 'internal models' (ref. 29). This is contrary to widespread assumptions concerning human movement organization, as mentioned above. We speculate that voluntary movements are, in general, organized by way of a simple representation of the perceptual goals[30], whereas the corresponding motor activity of, sometimes extreme, formal complexity is spontaneously tuned in. It may be this kind of movement organization that makes the richness and complexity of human voluntary movements possible, be it in sports and dance, skilful tool use, or language. □

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# Energetics of ion conduction through the K+ channel

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K+ channels are transmembrane proteins that are essential for the transmission of nerve impulses. The ability of these proteins to conduct K+ ions at levels near the limit of diffusion is traditionally described in terms of concerted mechanisms in which ion-channel attraction and ion–ion repulsion have compensating effects, as several ions are moving simultaneously in single file through the narrow pore[1–4]. The efficiency of such a mechanism, however, relies on a delicate energy balance—the strong ion-channel attraction must be perfectly counterbalanced by the electrostatic ion–ion repulsion. To elucidate the mechanism of ion conduction at the atomic level, we performed molecular dynamics free energy simulations on the basis of the X-ray structure of the KcsA K+ channel[4]. Here we find that ion conduction involves transitions between two main states, with two and three K+ ions occupying the selectivity filter, respectively; this process is reminiscent of the 'knock-on' mechanism proposed by Hodgkin and Keynes in 1955[1]. The largest free energy barrier is on the order of 2–3 kcal mol^{-1}, implying that the process of ion conduction is limited by diffusion. Ion–ion repulsion, although essential for

rapid conduction, is shown to act only at very short distances. The calculations show also that the rapidly conducting pore is selective.

The crystallographic structure of the KcsA K+ channel revealed that the pore comprises a wide, nonpolar cavity of 8 Å radius on the intracellular side, leading up on the extracellular side to a narrow pore of 12 Å that is lined exclusively by main chain carbonyl oxygens[4]. This region of the pore acts as a 'selectivity filter' by allowing only the passage of K+ ions across the cell membrane[4], whereas the wide cavity helps overcome the dielectric barrier caused by the cell membrane[5]. The translocation of K+ ions in single file through the narrowest region of the pore is expected to be the rate-limiting step in the conduction mechanism. This process can be represented schematically:

$$\text{K}^+ \quad \underline{\text{K}^+ \quad \text{K}^+} \quad \overrightarrow{} \quad \underline{\text{K}^+ \quad \text{K}^+} \quad \text{K}^+ \tag{1}$$
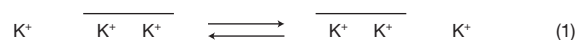
in which the approach of one ion from one side of the selectivity filter is coupled to the simultaneous exit of an other ion on the opposite side. Although such a concerted mechanism is consistent with long-held views of ion conduction through K+ channels[1–4], how it takes place at the atomic level remains unresolved. A simple calculation shows that the direct ion–ion repulsion varies by tens of kcal mol^{-1} when two or three ions are in the pore. Somehow, the K+ channel is able to exploit such large energies in a productive manner to yield a flux of about 10^8 ions s^{-1}. This implies that there is no significant activation free energy barrier opposing the concerted ion translocation. How can this be possible?

Although the available experimental data provide a wealth of information about the structure and function of K+ channels, theoretical considerations are necessary for understanding the energetics of ion conduction at the atomic level. One approach to refine our understanding of complex biomolecular systems is to use
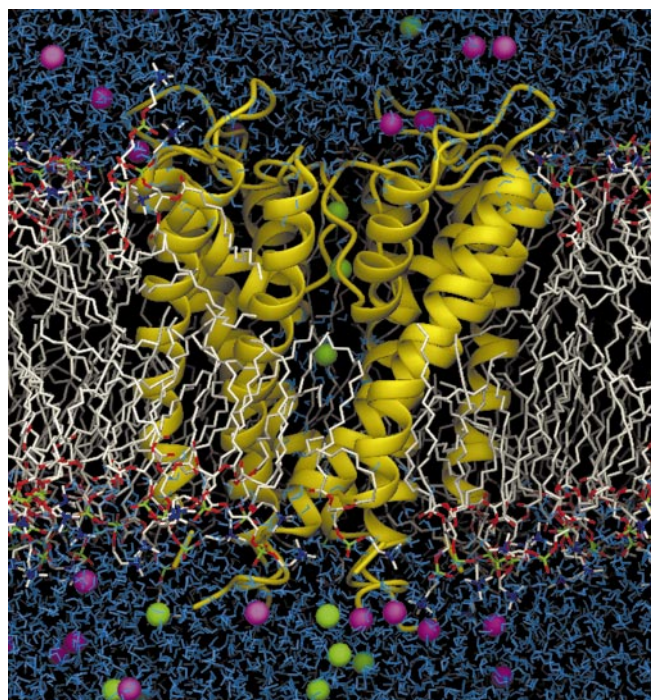

Figure 1 Molecular representation of the atomic model of the KcsA K+ channel embedded in an explicit DPPC phospholipid membrane bathed by a 150 mM KCl aqueous salt solution[11].

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