process in which CheW may also be involved. These signalling changes are diagrammed in Fig. B6. As all receptors affect the same pool of CheA kinase, the system responds to multiple stimuli as if it were exposed to the algebraic sum of the environmental changes.

Excitatory changes in kinase activity do not persist indefinitely because two related effects mediate adaptation, restoring the stimulated receptor to its null signalling state by creating compensating alterations in methylation. One action affects stimulated receptors specifically and persistently, the other affects methylesterase activity globally and transiently. For example, positive stimuli reduce CheA kinase activity and thus the content
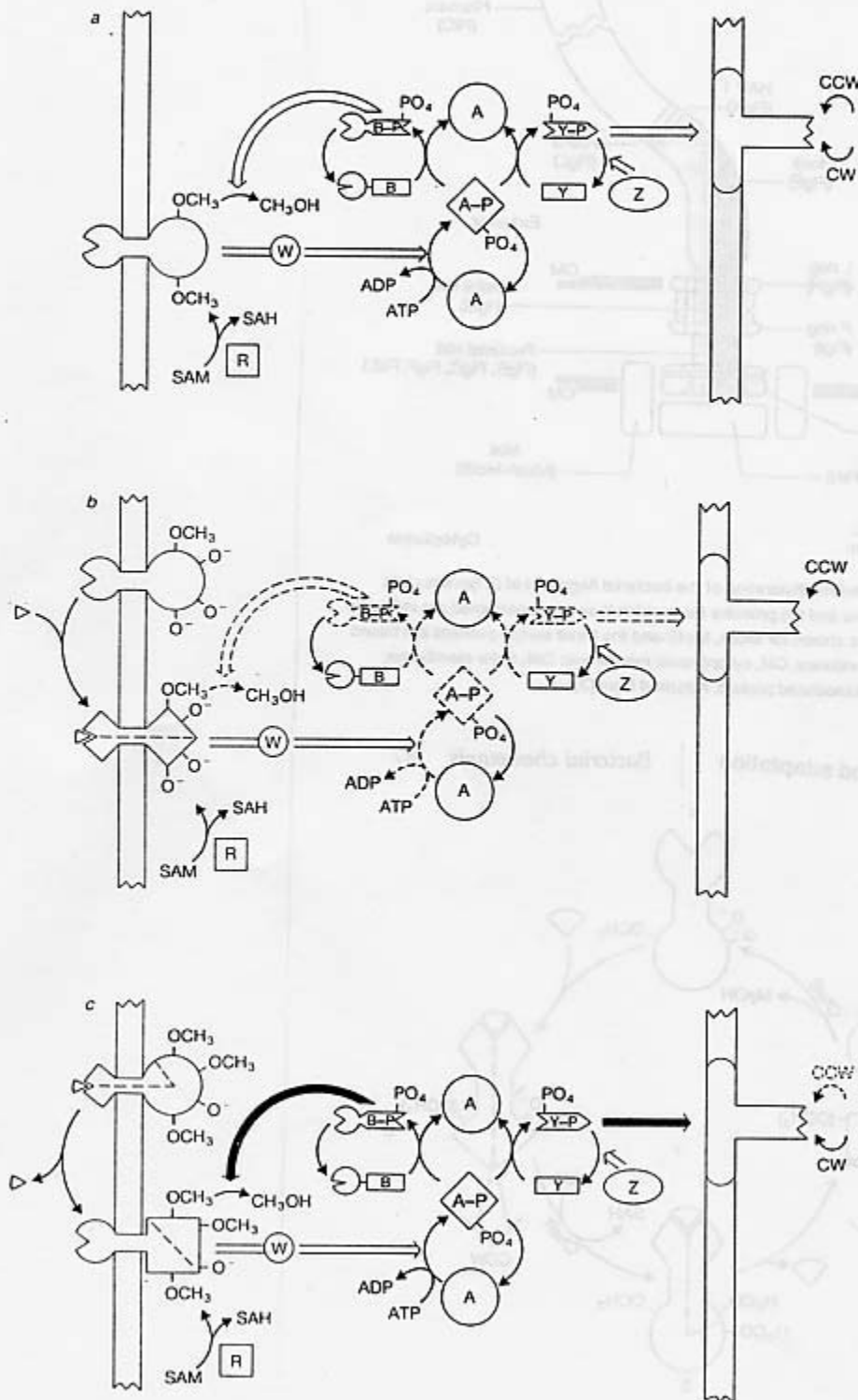
Fig. B6 Intermolecular signalling between chemosensory receptors and flagellum in bacterial chemotaxis. A schematic diagram of the protein–protein interactions and phosphotransfer reactions that link receptor to flagellum and that mediate sensory adaptation. a, The intermolecular circuitry. Phosphorylated CheY interacts with the flagellar machinery to produce clockwise (CW) rotation. Unphosphorylated CheY does not interact with the flagellar motor, leading to counterclockwise (CCW) rotation. In the unstimulated state a balance between phosphorylation and dephosphorylation of CheY results in a steady-state pattern of CCW rotation, leading to runs, and CW rotation, leading to tumbling. b, Binding of attractant to receptor leads to a decrease in CheY phosphorylation and a predominantly CCW rotation, thus decreasing tumbling. c, A decrease in occupancy of the receptor delivers a negative signal that results in increased CheY phosphorylation, and a predominantly CW rotation, increasing tumbling. The receptor protein is symbolized as in Fig. B4. Dotted arrows indicate decreased activities, thick arrows indicate increased activities. CheA, CheB, CheW, CheY and CheZ are indicated by the last letter of their names: phosphorylated forms are indicated by both a phosphate group on the shape representing the protein and a 'P' appended to the name.