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The Spinal Frog Takes into Account the Scheme of Its Body During the Wiping Reflex

Abstract. *The hindlimb of the spinal frog produces a wiping reflex evoked by electrically or chemically stimulating distal skin of the forelimb. The reflex was released in frogs supported on a flat surface or suspended. It was found to have two stages. During the first, the frog fixed the hindlimb in an intermediate posture irrespective of forelimb position. In the second, the movement depended on forelimb position, which determined the final posture of the hindlimb. In this final posture, all joints except the hip joint were fully extended; the hip angle was correlated with forelimb position and varied on repeated wipings. When the stimulus was applied to the skin of the back, the pattern of final postures was the same, but the intermediate postures differed. The organization of the wiping reflex is discussed in light of the hypothesis that movement is evoked according to changes in the equilibrium (postural state) of the system.*

Since the last century, it has been known that the spinal frog can remove a stimulus from the body skin by coordinated movements of the limbs (*1-3*). Pflüger (*3*), astonished at the perfect nature of this reaction, the "wiping reflex" (WR), supposed the existence of a sort of "spinal soul." Even a completely deafferentated limb can perform an effective WR (*4*).

The WR has been used to test motor behavior in ontogenesis (*5*), to study interrelations between skin and neurons (*6-9*), to analyze the influence of descending systems on the motor functions of the spinal cord (*10*), and to reveal the possibility of learning in the spinal frog (*11*).

The spinal frog can also remove the stimulus from the skin of the contralateral hindlimb or the ipsilateral forelimb (*4, 9, 10*). Since the stimulated limb may take various positions, the coordinates of the same stimulated spot will differ in space. We decided to analyze the cinematics of the respective movements.

The spinal cords of 15 frogs anesthetized under ether were transected at the level of the calamus scriptorius. The frog was placed in the refrigerator for 2 to 4 hours or until the next day, when the experiments were performed. The transection was checked by the absence of the head skin reflexes. After the experiments, the frogs were fixed in Formalin; then we verified the transection visually through a craniotomy. The experiments were carried out on frogs that were either suspended or supported on a flat surface. In the latter case, the head of the frog was pinned down, and the forelimbs and one of the hindlimbs were stretched out by threads to limit their movements.

The WR was evoked by local electrical stimuli or by chemical stimuli. The electrical stimulation was bipolar (interelectrode distance, 0.2 mm; duration of pulse, 0.5 msec; frequency, 30 pulses per second; current, 0.05 to 0.5 mA). The chemical irritation was evoked by applying a filter paper soaked in a 2 to 5 percent solution of H_2SO_4 (*4*). The movie camera above the frog's back registered its movements against the background of the measuring grid.

Figure 1 shows the movement of the most distal point of the hindlimb in the suspended frog in response to electrical stimulation of the forelimb. Trajectories are shown for two positions of the forelimb. In both cases, the same spot on the skin was stimulated, but its position in space changed by about 2.5 cm. In both cases, also, the movements were successful and the stimuli were removed. The movements started with the flexion of the whole limb, bringing the tips of the toes to the base of the forelimb (frames 8 to 10 for one movement and 5 and 6 for the other). The frog preserved this intermediate posture for 100 to 200 msec. During this stage, the immobility of the toes as well as of the whole limb was maintained. The intermediate posture was independent of the position of the forelimb, but further decisive ballistic movement depended on forelimb position. The movement by the toes to remove the stimulus led to a new posture (frames 14 and 15 for one movement and 11 and 12 for the other). During this final posture, all joints of the hindlimb were almost fully extended except the hip; its angle depended on the position of the stimulus in space. At the end of the WR, the paw returned to its initial position.

With electrical stimulation, no repeated movements were observed, whereas with chemical stimulation they did take place. As a rule, the first movement was the most precise one, and the number of

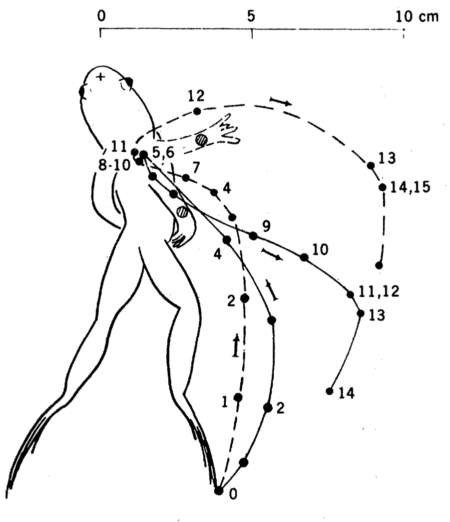

Fig. 1. Movements of the hindlimb in a suspended spinal frog during the WR evoked by electrical stimulation of the forelimb (hatched circle). The forelimb is shown in two different positions. Dashed and solid lines represent trajectories of the hindlimb when the forelimb was set into the upper or lower position, respectively; frames (16 per second) are numbered from the beginning of movement. The cross marks the point from which the frog was suspended.

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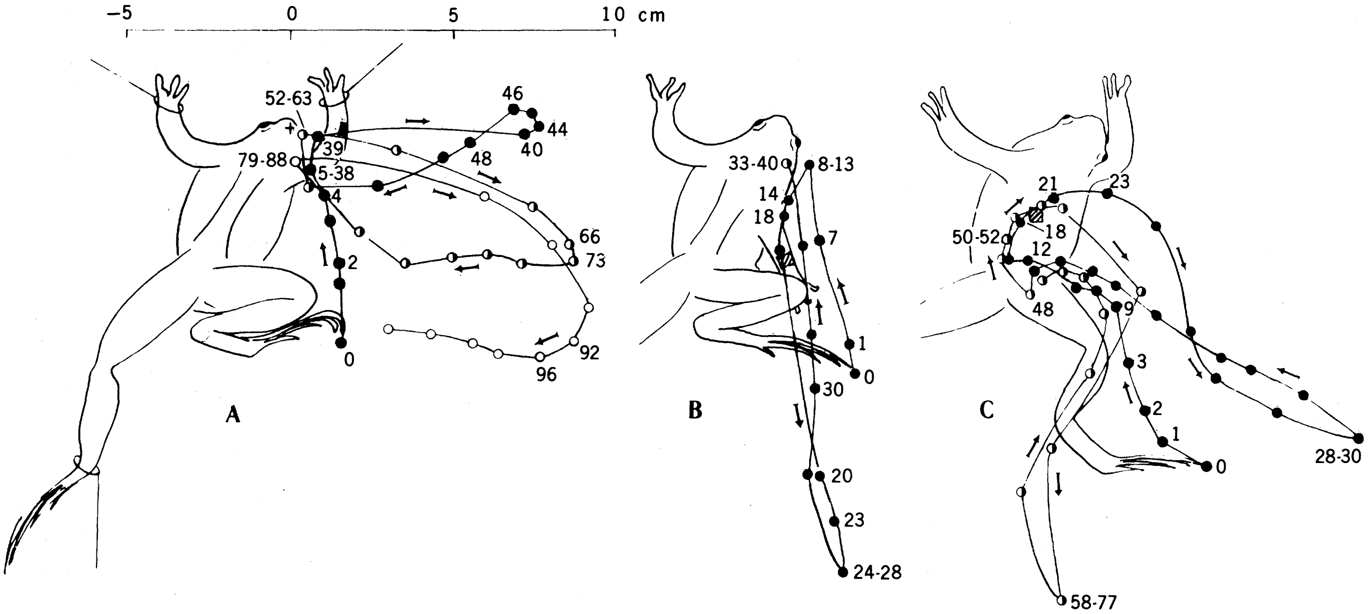

Fig. 2. Movements of the hindlimb in spinal frog lying on a surface during the WR evoked by chemical stimulation (hatched square) of the forelimb in different positions (A and B) or of the trunk (C). Filled, half-filled, or open circles represent positions of the toe tips during the first, second, and third cycles of wiping, respectively; frames (32 per second) are numbered from the beginning of movement. The cross marks the point at which the frog was pinned.

repeated wipings increased with increasing concentration of the acid (Fig. 2, A and B). When the frog was fixed on a horizontal surface, the forelimb was fixed in different positions so that the location of the stimulated place in space changed by 4.2 cm. If the limb was placed in the forward position (Fig. 2A) and the chemical stimulus applied, the frog transferred the hindlimb by flexion into an intermediate posture with the toes at the base of the forelimb (frames 5 to 38), as suspended frogs had. This posture was preserved for some time (for different frogs from 30 msec to 3 seconds). This was followed by a rapid transition to a final extensor posture. During the transition, the acid paper was removed by the tips of the toes. The final posture was held about 200 msec (frames 40 to 46). Repeating the movement, the frog rapidly recovered an intermediate posture (not the initial one); it preserved this posture for about 340 msec (frames 52 to 63). Then again the hindlimb rapidly moved to a different posture. The differences in the final postures of the whole limb were determined by the difference of the angle in the hip joint only. In any final posture all other joints were extended. The frog performed the first two movements precisely. The third movement became faulty, and then the paw resumed its initial position.

When the stimulated forelimb was fixed in the proximity of the hindlimb (Fig. 2B), the frog again flexed the hindlimb, transferring it to its previous intermediate position (frames 8 to 13 in the first movement and 33 to 40 in the repetition). The movement that removed the stimulus led to the final posture (frames 24 to 28), which was characterized by the extension of all joints except that of the hip. The angle of this joint varied during repeated wipings. These findings show that the WR was carried through in two stages. In the first stage, the intermediate position of the hindlimb is established irrespective of the forelimb position. The hindlimb extension of the second stage, however, is a function of forelimb position (Fig. 3). Postures A and B refer to the forward position of the forelimb, and postures C and D to its lower position. The hip angles of postures A and B are smaller than those of postures C and D. One may hypothesize that central commands that define the final hip angle essentially determine the direction of the decisive movement.

As long as the stimulus is applied to the back skin but not to the limb, there are other intermediate postures of the hindlimb (Fig. 2C, frames 12 to 18 for the first movement and 50 to 52 for the repeated one). The final postures (frames 28 to 30 and 58 to 77) are also characterized by full extension of the hindlimb; they differ in the hip angle when the stimuli are applied to the forelimb. There is thus every reason to suggest that all final postures constitute a one-dimensional set.

The frog's jump is realized by a rapid extension of all hindlimb joints. One can hypothesize that during the jump a certain subset of the WR programs is realized, the one which determines the final postures during the WR's.

The ability of the animals to carry out complex corrections of their movements was traditionally thought to be the function of higher levels of the brain—the cerebellum and cortex in particular. Lately, however, this point of view has been questioned. The spinal animal is capable of a delicate tactile reaction, the placing reaction, which had been thought to require the cortex (*12*). The spinal animal can display fairly complex corrections during locomotion as well (*13*, *14*). Our results show that the spinal frog can make complex leg movements according to the scheme of the body. It has been reported that the spinal frog is incapable of removing the chemical stimulus from the hindlimb which is stretched out (*4*). If this hindlimb is allowed to flex, however, both hindlimbs begin the WR. We have also observed in some spinal frogs that if we stretch the hindlimb by hand, the frog pushes the hand with its contralateral paw. In principle, therefore, the spinal frog is capable of removing the stimulus from the hindlimb no matter what its position is. It is possible that during the WR the nervous system takes into account not only the position of the stimulated limb but also the degree of the body's curve.

That the WR takes place whether the frog is in a horizontal or a vertical position demonstrates that the motor program provides sufficient stiffness of the hindlimb that the influence of gravity on the movement is minimized. This might

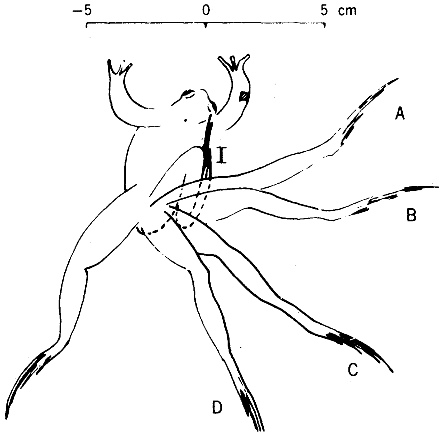

Fig. 3. An intermediate (*I*) and four final postures (A to D) of the hindlimb during the WR in the frog shown in Fig. 2. Not all final postures are displayed. If the forelimb is placed in the forward position, the ultimate position of the hindlimb is at A or B; otherwise postures C or D are taken.

be achieved if flexor and extensor motor neurons are activated not only reciprocally but also simultaneously, as occurs during human elbow movements (*15*). The WR directed to the trunk skin remains effective after deafferentation of the hindlimb (*1*, *4*). The central coactivation of the antagonistic motor neurons is likely to guarantee sufficient stiffness of the movement in this case as well.

Because the frog's hindlimb takes an invariant intermediate posture, at the next decisive stage, the movement no longer depends on the initial position of the leg; motor exactness is thus considerably increased. This mechanism is necessary because there is no time to correct the movement at the final stage: the transition from the intermediate posture to the final one takes 30 to 60 msec in some cases, so that the motor program is likely to be modified only during the preparation for the next wiping. The turtle is another animal that has some mechanism to diminish the dependence of the WR on initial conditions (*16*).

In both theoretical and experimental papers (*15*, *17*–*19*) the nervous system has been hypothesized to control a movement first by static characteristics of muscles (muscle torque, joint angle). An intersection of the flexor and extensor characteristics defines an equilibrium point of the joint. The central program determines a shift of the equilibrium point, and, as a result, the forced movement to a new equilibrium posture arises. The analysis of the WR shows the equilibrium postures. The choice of the intermediate equilibrium postures depends on the part of the body stimulated (limb or trunk). The choice of the final postures depends on the exact location of the stimulus in space. It is not yet clear whether the velocity of the transition from one equilibrium state of the system to the other may be controlled independently.

In warm-blooded animals such as cats and dogs, during the flexor phase of the scratch reflex (*20*, *21*) the limb occupies a position corresponding to the intermediate one in the frog. During the short extensor phase of scratching, the limb is likely to approximate an equilibrium state corresponding to the final extensor posture in the frog; in warm-blooded animals, however, this state is not achieved, because the central command soon returns the system to the intermediate posture. Thus we hypothesize that the mechanisms of the WR and of the scratch reflex are similar.

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Biological and Sociocultural Effects on Handedness: Comparison Between Biological and Adoptive Families

Abstract. Data from adoption studies on handedness indicate that the effects of shared biological heritage are more powerful determinants of hand preference than sociocultural factors. Biological offspring were found to show nonrandom distributions of right- and non-right-handedness as a function of parental handedness; these distributions were consistent with the results of previous family studies. In contrast, the handedness distribution of adopted children as a function of parental handedness was essentially random.

Despite more than 50 years of systematic scientific inquiry, the question of whether genetic factors are involved in the intergenerational transmission of handedness is still unresolved. Recently, Annett (*1*) reviewed genetic and nongenetic models for the inheritance of handedness and pointed out that few conclusions about genetic influences on handedness can be firmly drawn until the results of studies of hand preference in adoptees and their families are known. Collins (*2*) also has asserted that only a cross-fostering design will enable us to assess the importance of the early environment in the development of hand preference. If growing up in a right-handed world exerts an overwhelming bias toward right-handedness, one would expect to find few if any left-handers in families in which the parents are right-handed.

Studies of handedness in biological families have generally found that the proportion of non-right-handed offspring was greatest when neither parent was right-handed and was lowest when both parents were right-handed (*1*, *3*–*6*). Although some studies have found support for a maternal effect in matings in which one parent was right-handed and the other had a mixed or left-handed preference (*1*, *3*, *5*), others have failed to confirm such an effect (*6*).

In this study, I assessed hand preference in three samples of adopted children and their adoptive parents and in two control groups of biological relatives. The results are considered in the context of the existing literature on fam-

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