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Phase-dependent reflex modulation in tibialis anterior during passive viewing of walking

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ABSTRACT

It is well established that reflexes are highly adaptive, as they depend both on our intention and on the active state of the muscles. Reflex gains change dynamically during actions such as walking and running, with the gain of cutaneous reflexes being increased at the end of the stance phase but decreased at the end of the swing phase in the *tibialis anterior* (TA) muscle. Reflex gains can even change during the mere observation of an action. The mechanisms and functions of such modulations are unclear. It has been suggested that the changed reflex gains prevent the actual performance of actions that we see. However, the modulation of reflexes in response to seeing an action has never been reproduced for the active execution of such actions. In the present study, medium-latency cutaneous reflexes from the TA muscle, of which the activity and reflexes during walking are well known, were measured in human subjects. The results show that the gain changes of the medium-latency responses of the TA are the same as during active walking. We conclude that reflexes do not represent an inhibitory mechanism that prevents motor output during action observation. Instead, our findings provide evidence that even the peripheral spinal motor system is actively involved in the motor resonance processes, without evoking any measurable motor responses.

1. Introduction

It has been known since the 1970s that reflex responses are not stereotypic but depend in a functional manner on the direction of the perturbation (Marsden, Merton, & Morton, 1972), even if a distant part of the body is perturbed. Moreover, such postural responses are known to depend on the current task (Marsden, Merton, & Morton, 1981). Reflex responses can be generated in several leg muscles in humans by electrical stimulation of cutaneous afferents of the foot (Hugon, 1973). Studying these reflexes, it has been found that reflexes do not only depend in an adaptive way on the perturbation, but also change dynamically with the phases of a voluntary action such as walking. In cats (Forssberg, Grillner, & Rossignol, 1975) and in man (Yang & Stein, 1990) these properties, from the servo action to the dynamical behavior, make reflexes invaluable for a stable motor control. Whereas reflex behavior has become firmly rooted in motor control, it has become clear that the motor system interacts intensively with perception. For example, seeing someone grasp, will recruit grasping neurons in the premotor cortex (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). It has therefore been hypothesized that extracortical motor control networks should adverse this mirror-like behavior in the motor cortex, in order to prevent that we always make the movements that we see (Baldissera, Cavallari, Craighero, & Fadiga, 2001; Rizzolatti & Craighero, 2004). There is experimental evidence from Hoffman reflexes (H-reflexes) evoked during the observation of grasping movements that interpreted in this manner (Baldissera et al., 2001, but see Montagna, Cerri, Borroni, & Baldissera, 2005). The H-reflex of the *soleus* muscle is also modulated if the subject observes leg movements, but it is not known whether these changes are dynamic, nor if they are related to the observed act (Cheng, Tzeng, Hung, Decety, & Hsieh, 2005). However, there is experimental evidence that the observation of a postural perturbation can evoke a postural response in the observer (Tia et al., 2011).

Reflexes are rapid neural responses of the peripheral motor system to perturbations or to kinematic deviations from the intended posture or movement. As such, reflexes can be regarded as an expression of an extended motor plan, that encodes how to reach the desired goal, given the possibility of unpredictable events and deviations from the desired movement. This has for example been formulated as equilibrium-point control (de Lussanet, Smeets, & Brenner, 2002; Feldman, 1966; Feldman, Ostry, Levin, Gribble, & Mitnitski, 1998). Indeed, evidence suggests that the cortical representation of movements encodes the movement goal, independently of the current body posture (Graziano, Taylor, & Moore, 2002). For stable control it is vital to respond rapidly, and therefore we expect that spinal mechanisms are likely to be recruited along with cortical motor activity, even if the subject has no intention of actual motor action.

There are no direct measurements of the dynamic modulation of evoked reflexes during grasping movements. Instead, we selected walking movements because the dynamics of evoked reflexes are well

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documented (e.g. Duysens, Bastiaanse, Smits-Engelsman, & Dietz, 2004; Duysens, Tax, Murrer, & Dietz, 1996; Duysens, Trippel, Horstmann, & Dietz, 1990; Pijnappels, Van Wezel, Colombo, Dietz, & Duysens, 1998; Yang & Stein, 1990). Thus, we hypothesized that reflexes evoked to the *tibialis anterior* (TA) muscle, by cutaneous electric stimulation of the posterior tibial nerve, change dynamically with the phase of visually presented walking stimuli. Furthermore, we expected that the gain of the evoked reflexes of the TA muscle modulates dynamically with the phase of visually presented walking, as if the observer would actually walk actively. Third, we hypothesized that the visual observation of walking stimuli should not result in any changes in the EMG of leg muscles, specifically in the TA muscle.

2. Material & methods

Fourteen healthy, right-handed subjects (28.9 ± 5.3 years; six females) gave written, informed consent prior to participation. The study protocol was approved by the local ethics committee and conformed to the declaration of Helsinki.

2.1. Set-up

As visual stimulus displaying human walking we used point-light biological motion (Johansson, 1973). The visual perception of biological movements from moving point-light stimuli has been intensively studied. Such point-light biological motion is devoid of image information but is nevertheless easily recognized. Depending on the task, it activates the sensorimotor representations in the brain (Buccino et al., 2001; de Lussanet et al., 2008; Michels, Kleiser, de Lussanet, Seitz, & Lappe, 2009; Saygin, Wilson, Hagler, Bates, & Sereno, 2004). This system has a central role in the observation of active body movements; it is active during action execution as well as during action recognition (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Jeannerod, 2001).

In order to construct the point-light stimulus, 3-D recordings (Qualisys, Gothenburg, Sweden) of the main joints of a male actor walking on a treadmill at 3.5 km/h (0.97 m/s), 0.877 walking cycles per second, were fed into an iBook computer running an in-home programmed application (MotionViewer, version 48.111123, using XCode 3.1 and OpenGL). The visual stimulus presented a slightly oblique back-view of walking (slanted to the right by 13°) which measured 6 × 15 cm on the 22″ TFT display that was connected to the iBook. To ensure that the observers perceived the stimulus as a back-view, the markers were occluded when covered by body parts.

Via the USB port, the iBook was also connected to the electrical stimulation device (Digitimer DS7A, Welwyn Garden City, UK). By this, the stimulus program also triggered the electrical stimulation. The stimulation electrode (Axelgaard, Fallbrook, CA, USA) was placed at the medial side of right ankle, where the posterior tibial nerve is closest to the skin (Roby-Brami & Bussel, 1987). Trains of 5 biphasic rectangular pulses each of 1 ms duration at 200 Hz were then applied with the constant-current stimulator. During quiet standing, the motor threshold was determined by gradually increasing the stimulus intensity until a visible muscle contraction was elicited in the *m. abductor hallucis*. The stimulation intensity was set on 1.5 times the motor threshold (Yang & Stein, 1990). The EMG of the right TA muscle was recorded at 2000 Hz using bipolar, amplified surface electrodes (Biovision, Wehrheim, Germany). The recorded signal was band-pass filtered (30-300 Hz), rectified and averaged using Matlab (Mathworks, Natick, MA, USA).

2.2. Procedure

The participants were instructed to remain fully relaxed while observing the visual stimuli attentively. They were requested not to focus on single details but on the whole figure. The subject had to keep up with the phase of the walking stimulus. The latter instruction was important to ensure that the perceived action was timed to the stimulation.

The subject was sitting comfortably in front of the computer display that presented the point-light stimuli. Before the experiment started, each participant saw the walking stimuli for 5 min to get accustomed to the task. The experiment consisted of 39 trials in randomized order, 13 for each condition. Each trial lasted 10 s (8.8 walking cycles), with a 10-s interval presenting a blank screen. The posterior tibial nerve was electrically stimulated during the second half of each trial at an unpredictable time (i.e., during one of the last 4.4 walking cycles). The subjects were not told that the stimulation was timed with respect to the walking phase. For the presented walking this was either at the end of a stance phase or at the end of a swing phase of the right leg of the point-light display, triggered by the stimulus software. The definition of the phases in the stimulus was as in Duysens, Tax, Trippel, and Dietz (1992). In the baseline condition, the subject's task was the same, but instead of a walking persona scrambled version of the walking stimulus was presented (de Lussanet et al., 2008).

2.3. Analysis

Cutaneous electric stimulation on the foot elicits reflex responses in many muscles (Hugon, 1973). These responses, starting from about 75–80 ms are known as P2 responses. The data analysis was kept analogous to the established methods for active walking (Duysens et al., 1990; Duysens et al., 1996; Yang & Stein, 1990). The recorded walking cycle was divided in 16 periods (each lasting 71 ms). The relevant phases were 9 and 16 (end of stance phase and end of swing phase of the right foot) (Van Wezel, Ottenhoff, & Duysens, 1997; Yang & Stein, 1990; Zehr, Komiyama, & Stein, 1997).

The reflex responses were quantified by calculating the integral of the root mean square (RMS) of the EMG signal of the time window between 80 and 130 ms from the beginning of the electrical stimulation (Pijnappels et al., 1998). For each subject the mean reflex responses for the two walking phases were normalized to the baseline condition. Reflex enhancement was defined as the percentage increase of the RMS signal with respect to the baseline and reflex suppression as the percentage decrease of the RMS signal.

The presence of phase-dependent EMG activity in the TA during the passive observation of walking would be problematic for the interpretation of our data. When studying the phase-dependent modulation of reflexes it is important to realize that the amplitude of the evoked responses often varies primarily as a result of the changes in background activity ("automatic gain control" — Matthews, 1986). That is why, additionally, the activity in TA in the mean observed step cycle of every subject (we used 78 steps per subject) without electrical stimulation was also calculated. The mean EMG values for phase 9 and 16 of each subject were used for that.

3. Results

Fig. 1 shows the averaged EMG responses to evoked reflexes of the TA muscle of four representative subjects. Twelve out of the fourteen subjects showed a stronger effect for the end stance phase than for the end swing phase. The upper right panel shows the traces of one of the two subjects who did not. The baseline condition was intermediate in some subjects (upper left panel) but not in all (the other three examples).

When electric stimulation was applied at the end of the displayed stance phase, the evoked P2 responses in the right TA muscle (ipsilateral to the standing foot in the display) were higher on average than those evoked at the end of the displayed swing phase (Fig. 2). The modulation depth was 31.9%: with respect to the baseline condition the P2 responses were reduced by 5.4% (±20.9% standard deviation) at the end of the stance phase and enhanced by 25.5% (±26.6% standard deviation) at the end of the swing phase. The one-tailed paired t-test performed on the normalized responses showed that the modulation of the P2 responses was significant ($t(13) = 2.4$, $P = 0.017$).

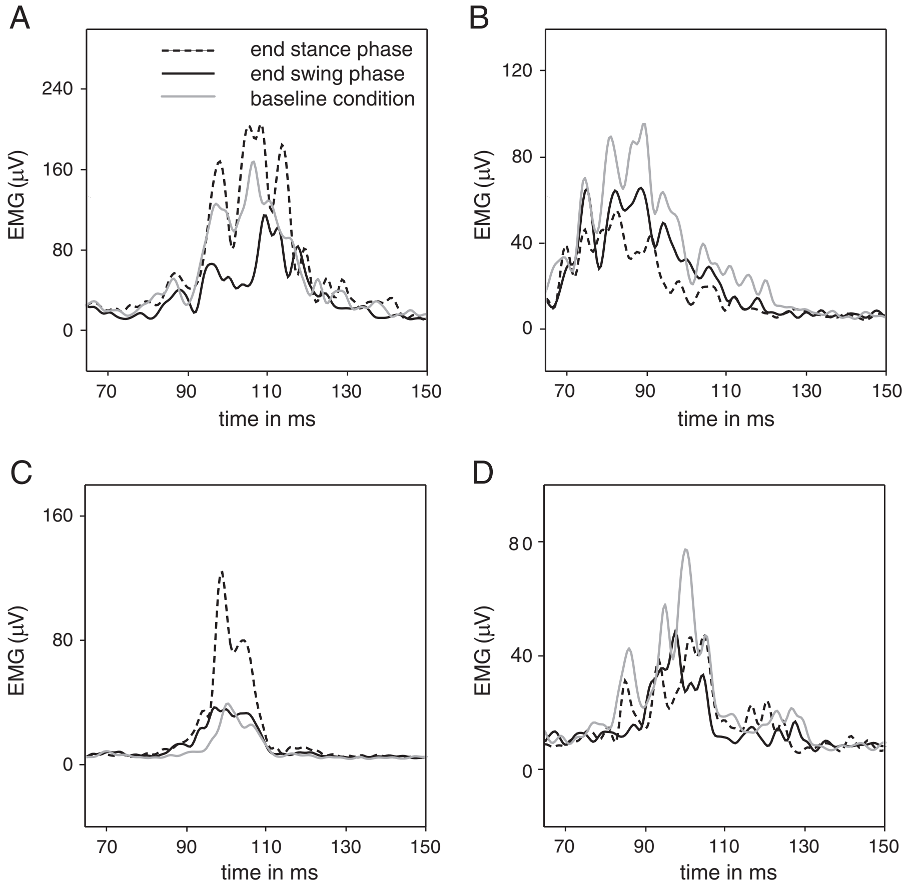

Fig. 1. Mean EMG of the *m. tibialis anterior* (TA) for four subjects (thirteen repetitions per trace). Continuous black trace: stimulation at the end of presented swing phase; dashed trace: stimulation at the end of presented stance phase; gray trace: stimulation during baseline condition. Time is from the onset of electrical stimulation.

Without electrical stimuli, none of the subjects had an increased EMG activity in the TA muscle during the mere observation of walking. The two-tailed paired t-test revealed that there was no systematic modulation with the phase of the observed walking cycle in the background EMG (t(13) = −3.2, P = 0.75; Fig. 3).

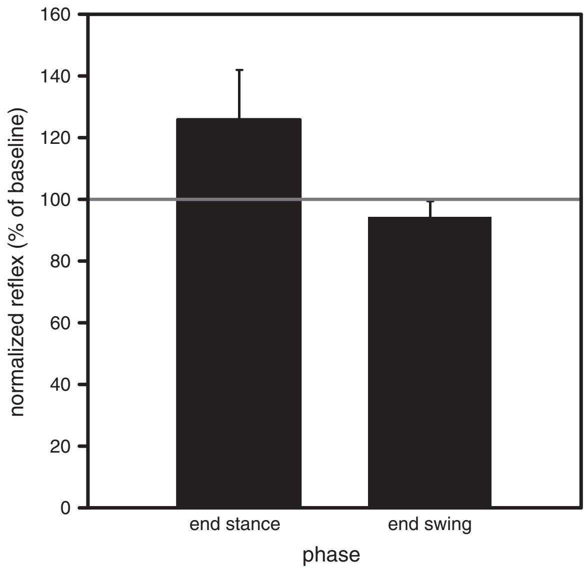

Fig. 2. Mean (RMS after rectification) normalized responses of fourteen subjects, with standard errors. Horizonal line: baseline condition.

4. Discussion

This is the first study to give direct evidence that the reflexes during passive observation of an action and during active execution of the same action modulate in the same manner. The results show that there is a close relationship between the TA reflex responses and the phases of the step cycle of the observed point-light walker during electrical stimulation, i.e., that the reflex behavior was in accordance with the usually found responses in TA during self-performed walking. While it is well established that the cortical excitability is enhanced during passive observation of another person's actions, earlier evidence seemed to indicate that the modulation of the spinal excitability is opposite to the modulation of the cortical excitability (so as to prevent automatic imitation) (Baldissera et al., 2001).

The crucial difference with earlier studies is that we studied an action for which the dynamic modulation of the reflexes is extremely well documented so that we can be confident that our findings correspond both qualitatively and probably even quantitatively with the modulation during active execution. For the grasping movements (Baldissera et al., 2001; Montagna et al., 2005), reflexes have never been measured during active execution. On the other hand, Cheng et al. (2005) did not find significant differences in the evoked reflexes for passive viewing of stepping nor between heel- and toe-stepping movements, which might be due to methodological issues. Cheng et al. did find enhanced reflexes depending on the leg that was turned to the observer for standing still, showing that attending to one leg enhances the reflex responses in the corresponding leg of the observer. Note that the subjects in the present experiment saw the walking stimuli from behind, and were instructed to concentrate on the whole stimulus rather than on a local feature.

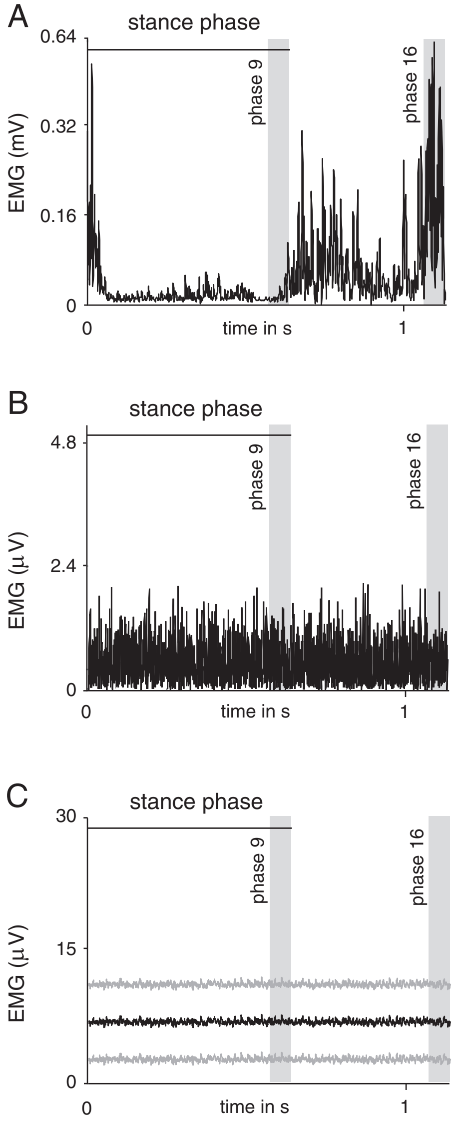

Fig. 3. A. EMG pattern of a typical stride cycle of the ipsilateral TA muscle for one representative subject during active, normal walking. B: Mean ipsilateral TA EMG of 78 observed strides for the same subject, on a 133 times inflated scale. C. Mean ipsilateral TA EMG of all subjects (black graph), with ±1 SD (gray curves). The gray bars show phase 9 and phase 16 of the walking cycle.

One may object that walking movements differ from grasping in that walking is rhythmic and less controlled by the brain. If we assume this true, then our findings are much stronger than an equivalent finding for grasping would be. Since the modulation of the reflex responses is thought to be a predominantly spinal mechanism, it is striking that visual perception can play a role even at that level.

One might also object that electrically evoked responses are much too artificial to have any relevance for normal motor control. However, there is a large body of literature to show that the control of movements to all kinds of perturbations is a continuous and dynamic process (e.g., Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). Thus, electrically evoked reflexes just reflect the normal control of movement in the presence of unpredictable perturbations in an experimentally well controlled setting. The use of electric over mechanic perturbation (e.g., Marsden et al., 1972; Marsden et al., 1981) is obvious: the temporal and spatial precision is much higher for electrical perturbations. Finally it is to be remembered that the modulation of a reflex gain need not evoke any action by itself, as long as the reflex is not triggered by a perturbation or a central command (or a supra threshold TMS pulse).

Although the reflex modulation is a well-studied and well-established effect, it is also well accepted that not all participants show this modulation during walking. This fact is well documented in the literature (Baken, Nieuwenhuijzen, Bastiaanse, Dietz, & Duysens, 2006; Duysens et al., 1990; Duysens et al., 1992; Hoogkamer, Massaad, Jansen, Bruijn, & Duysens, 2012; Van Wezel et al., 1997; Yang & Stein, 1990). That two out of fourteen of the present study did not show the effect thus appears to be in line with the data for active walking. Still it will be interesting to find out whether the same subjects lack the effect in both walking and the observation of walking.

In agreement with our expectations (see section Analysis), we did not find a systematic modulation of the EMG with the phases of the observed walking cycle in any of the subjects (Fig. 3B, C). Although there is little statistical power due to the relatively small number of subjects, the absence of any trend is convincing and is in line with a study that also could not find any observation related muscular activity (Cheng et al., 2005; Mulder, de Vries, & Zijlstra, 2005).

It has been a highly influential finding that the premotor cortex is active during the passive observation of actions (Rizzolatti et al., 1996). Although such activity in the premoter cortex does not necessarily result in muscular activity, it is well-known that mirroring movements are easily evoked. For example, the threshold for evoking a mirror movement by transcranial electromagnetic stimulation (TMS) in the premotor cortex is lowered with respect to not observing the action (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). However, visual observation of action has only been found to activate the cerebrum and cerebellum (Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). The absence of muscular activity (Rizzolatti et al., 1996) and the apparent negative modulation of the H-reflex for grasping (Baldissera et al., 2001) has been interpreted such that spinal processes are deactivated and not involved in the mirror process of movement observation. The present finding, that reflex gains are modulated dynamically during the visual observation of a highly automated motor action such as walking shows that even the spine is actively involved in such a cognitive visual task. While it is well established that reflexes evoked by cutaneous stimulation have cortical components, it is also widely agreed that spinal control has a major contribution (Duysens et al., 2004).

Our data support a novel view at the motor control of walking. To date, there is uncertainty about the underlying mechanism of phase-dependent reflex reversals. It has been proposed that this dynamic modulation is caused by interactions between afferent inputs, a property of a locomotor pattern generator (Duysens et al., 1996), or it might reflect an influence by supraspinal input (Duysens et al., 2004). The latter is supported by findings that report a strong control of the TA by the motor cortex (Pijnappels et al., 1998). The supraspinal input from the motor cortex is much stronger for the TA than for the *m. soleus*, which in turn is supposed to depend more strongly on peripheral reflexes (Dietz, 1992; Schubert, Curt, Jensen, & Dietz, 1997). A further study that measured cutaneous reflexes in healthy subjects walking passively on a treadmill with a Driven Gait Orthosis (DGO) is also in line with that (Duysens et al., 2010). Such DGOs usually produce abnormal ankle trajectories and hence a changed muscular activity. Additionally, there is a constant pressure on the sole throughout the step cycle. With respect to the found absence of suppression of reflexes at end swing, the authors proposed a dominant role of either spinal (CPG) or of cortical input. As the subjects of the present study sat quietly and showed no modulations in their EMG, the modulations of the P2 responses must have originated from supraspinal influences. This also suggests a prominent role of supraspinal sources on the modulation of reflexes in normal walking.

The present data seem to contradict a finding that measured a dynamic modulation of spinal excitability during the observation of hand actions (Baldissera et al., 2001). H-reflexes of a finger flexor muscle (*m. flexor digitorum superficialis*) were reported to be inhibited during the observation of finger flexion and facilitated during finger extension, which is opposite to the muscular activity in this finger flexor muscle during the same action when actively performed. However, the modulation of reflex gain to seeing an action has never been measured for a condition in which it is known how the gain changes during active execution of the action, and it has been suggested that this modulation during observation might be the same as during active execution (Montagna et al., 2005). We found that reflexes in the TA muscle are modulated in just the same way as during active walking (this is a decreased response at the end of the swing phase and an increased response at the end of the stance phase).

The spinal cord is not just a functional unit that executes motor plans generated by higher motor networks, but is interacting continuously with motor cortical areas in the initial phases of preparation for movement. As such it contains cervical interneurons that show preparatory patterns before execution of a movement in tasks that involve an instructed delay period (Prut & Fetz, 1999). While cortical premotor neurons show an increased activity in this period, many of the cervical interneurons follow an inhibitory pattern, which is proposed to reflect the suppression of the initiation of a movement. It has therefore been suggested that this represents a general descending inhibition during the preparatory period (Fetz, Perlmutter, Prut, Seki, & Votaw, 2002).

If reflexes do not prevent the automatic reproduction of actions that we see, it remains an open question how we prevent such automatic copying of actions. One such mechanism might be provided by hypothetical brain circuits responsible for inhibiting motor output during action observation (Gangitano, Mottaghy, & Pascual-Leone, 2008; Jeannerod & Anquetil, 2008). A different explanation might be derived as follows: only about one third of the premotor neurons have mirror properties (in monkeys, Gallese et al., 1996). It is known that there are direct projections from the premotor cortex to the spine (Dum & Strick, 1991; He, Dum, & Strick, 1993). Also it is known that stimulation of premotor neurons can evoke complex movements in monkeys (Graziano et al., 2002) and man (Fadiga et al., 1995), but it is not known whether and how the populations of mirror neurons play a role in this. Thus, on the basis of these data, one could hypothesize that neurons with mirror-like properties modulate the spinal reflex gains and do not project directly to the α motor neurons in the spine. If these neurons thus do not initiate actions, but predominantly have a modulatory input on spinal networks, there would be no need for a mechanism that prevents the execution of actions that we observe.

The result has important implications. It means that it is further unclear how we prevent ourselves to automatically perform the actions that we see (as we explained above). On the contrary, the evidence now shows that spinal excitability can increase both for middle-latency reflexes (our study) as well as for short-latency H-reflexes (Baldissera et al., 2001; Montagna et al., 2005) without evoking any motor responses (Fig. 3). Moreover, the meaningful modulation of reflex gains might have important social functions, known as motor resonance mechanisms (Prinz, 1997). For example, it might provide a mechanism to explain why humans tend to walk in phase, because the seeing of the walking of the others automatically tunes the spinal response pattern to the same phase. Also, it might be a valuable aid in motor learning by imitation, for if the observation of an action automatically prepares peripheral motor mechanisms for executing these observed actions, the cognitive level is freed to compute the fine adjustments for precise imitation. Further, the dynamic modulation of reflex gains during action observation might help to better understand the actions that we see at a motor level. For example, the dynamic change of spinal reflex gains might by itself provide afferent information about the spinal gain mechanisms which again might provide additional information about the movements that we observe visually. Thus, the modulation of reflex gains might be a true part of the chain for action understanding from visually presented stimuli.

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