Activation of carotid baroreceptors inhibits spinal reflexes in man

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Summary The present study was designed to investigate the effect of baroreceptors on a spinal reflex. The Achilles tendon reflex (T reflex), a monosynaptic spinal reflex, was chosen as an indicator of descending influences of central activation.

The baroreceptors are stretch receptors which respond to extensions of the arterial wall. Carotid sinus baroreceptors can be manipulated non-invasively by means of a cuff around the neck. In this study, the phase-related external suction (PRES) neck cuff technique was used. PRES applies short changes in cuff pressure as a function of heart cycle phase, controlling for non-specific effects found in other baroreceptor manipulation methods.

The T reflex was reduced when elicited during the highest levels of baroreceptor activation. Reflex amplitude was largest when elicited during the lowest levels of baroreceptor activation. These results are consistent with previous findings that baroreceptor activation reduces CNS excitability.

Key words: Baroreceptors; Achilles tendon reflex; Phase-related external suction (PRES); EMG

One major influence of cardiovascular activity on the brain is realized through the baroreceptors, which act on brain-stem vasomotor centers and by way of the tractus solitarius on further systems ascending from the brain-stem to the hypothalamus and probably to higher cortical regions. Apart from their representation in the insular cortex, the baroreceptors also influence cortical functioning through the ascending reticular activation system. Koch (1932) observed that baroreceptor stimulation led to sleep in dogs, and Cole (1989) extended this finding to humans. Bonvallet and Allen (1963) and Bonvallet et al. (1953, 1954) working with animals, and Vaitl and Gruppe (1992) in their studies of human subjects all observed that different methods of baroreceptor activation led to changes in the EEG power spectra associated with decreased arousal.

The tractus solitarius efferents have sympathetic and parasympathetic autonomic effects, with clear cardiac manifestations. The central damping of increases in blood pressure has behavioral consequences, such as the raising of pain thresholds (Rau et al. 1993a) and possibly anxiety reduction (Dworkin 1988).

In the present study we investigate the influence of descending baroreceptor effects on monosynaptic reflex activity. This builds on the findings of Schulte et al. (1959) that mechanical baroreceptor stimulation of cats led to a gradual elimination of spontaneous resting gamma motoneuron activity.

Baroreceptors are stimulated through changes in the stretching of the arterial wall. The natural stimulus for this change is an increase in pressure inside the blood vessel. The same stimulatory effect may be achieved through the application of subatmospheric pressure in the surrounding tissue. For the pressure receptors located in the carotid sinus this has been realized by means of a cuff around the neck. Many studies with humans (Eckberg 1976; Elbert et al. 1988; Rau et al. 1988) have contrasted the effects of continuous negative cuff pressure with continuous positive cuff pressure. The differential cuff pressure effects seemed not to be confined to differential effects on the baroreceptors but also to the differential effects on receptors in the skin, pharynx, etc. The experience of negative cuff pressure has been described by subjects as significantly less pleasant than that of positive pressure. Thus, both psychological and physiological processes may differ due to exteroceptive influences, resulting in an inadequate experimental control condition. On the basis of a suggestion by Dworkin (1988), we designed cardiac phase-related external suction (PRES), a neck suction technique which overcomes this critical shortcoming

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* Research was supported by the Deutsche Forschungsgemeinschaft (El 101/3).

(Rau et al. 1992). Using PRES, subjects cannot reliably discriminate between baroreceptor activation and control conditions (Furedy et al. 1993).

Because carotid stretch receptors are not only sensitive to static levels of pressure, but also to the rate of change of pressure, the same suction pulse will have different effects when applied to different time segments within the cardiac cycle (Eckberg 1976). PRES delivers short bursts of either negative or positive cuff pressure during either systole or diastole.

Hoffman (H) and Achilles tendon (T) reflexes can be used to estimate changes in the excitability of the motoneuron pools in man (Paillard 1955). There has been some controversy regarding the role of alpha and gamma motoneurons in the H and T reflexes (Burke et al. 1981). T reflexes are an index of alpha motoneuron output, which itself is the result of supraspinal and segmental afferent volleys to alpha and fusimotoneurons, whereas Ia afferents are also under presynaptic control (Hultborn et al. 1987a,b).

In the present study, the T reflex was chosen as a possible indicator of descending modulatory effects of baroreceptor activation, since we have investigated the supraspinal modulation of this reflex during preparation of an instructed response in earlier studies (Brunia and Boelhouwer 1988).

The T reflex is evoked by a tendon tap, stretching the calf muscles. The lengthening of the intrafusal fibers of the muscle spindle will discharge group Ia afferent fibers, which in turn have a primarily monosynaptic link to the alpha motoneurons. A sufficiently large depolarization of the motoneurons results in the contraction of the calf muscles.

Animal studies (Schulte et al. 1959) suggest that the afferent impulses from carotid sinus baroreceptors, reaching the brain-stem, also radiate to the somatic motor system, either suppressing reticular activation or activating the reticulo-spinal suppressors located in the same gross region.

It was hypothesized that the greatest T reflex differences would be found between conditions of highest baroreceptor activity (during PRES enhanced systole) and lowest baroreceptor activity (PRES enhanced diastole). It was also hypothesized that baroreceptor stimulation (systolic suction/diastolic pressure) would evoke a greater heart rate deceleration than the systolic pressure/diastolic suction condition, validating differential activation of the baroreceptor reflex.

Method

Subjects

Nine men and 3 women (19–58 years old), all free of cardiovascular abnormalities and medication, gave in-

formed consent. The study was approved by the human ethics committee of the University of Tübingen.

Procedure

The subject was comfortably seated in a specially designed chair, with the feet strapped to two foot plates. The knees were positioned with approximately 120° of flexion while the ankle was set rectangularly. After proper adjustment of the reflex stimulator, the cuff was fixed with a belt around the neck. Several applications of a positive and a negative pressure inside the cuff served to establish proper functioning and simultaneous heart rate recording assured that the baroreflex could be elicited. Two practice trials introduced the subject to the stimulation procedure.

Each subject received 64 computer controlled trials of 6 sec duration. Thirty-two trials with systolic suction/diastolic pressure and 32 trials with systolic pressure/diastolic suction were presented in a pseudo-random sequence. In each trial, T reflexes were elicited twice (after the first and fourth R waves) during the same heart period (systole or diastole). Thus, there were 4 different trial categories.

In trials with systolic T reflexes, the reflexes were elicited 200 msec after the detection of the first and fourth R waves; in trials with diastolic suction 100 msec after the first and fourth pressure reversals. Thus the interval between two reflex elicitations in any one trial, depending on the subject's heart rate, varied between 3 and 4 sec. The interval between two subsequent trials varied randomly from 13 to 23 sec in length. (Rather long intervals were chosen, as neural excitability is known to recover slowly after a reflex excitation.)

An MS-DOS computer programmed in ASYST was responsible for timing and initiation of experimental stimuli and for collection of the physiological data (heart rate and EMG).

Baroreceptor stimulation

PRES delivers short bursts of either negative or positive cuff pressure during either systole or diastole. Application of a negative pressure burst during systole adds to the pulse wave triggered dilatation of the vessel and enhances both the speed and the degree of the dilatation, leading the baroreceptors to fire more vigorously. The application of the same negative cuff pressure burst during diastole will not overlap with systolic dilatation, but will only delay the reconstriction of the arterial stretch. A positive pressure pulse follows suction, being applied during diastole in the case of systolic suction and during systole in the case of diastolic suction. The first situation enhances the amplitudes of the pulse wave triggered dilatation, the second flattens the effects of the internal pulse wave. The technical details of the construction and operation of PRES are described in Rau et al. (1992).

The pressure changes were triggered by the upstroke of the R wave of the electrocardiogram. Each time an R wave was detected, a Beckman 9806 cardiograph coupler generated a square wave pulse (Q output). This square wave was fed into the computer (via a TTL circuit attached to the digital input) which then determined the time (to within 1 msec) it took for the R wave to appear. For stimulation (systolic suction/diastolic pressure) the cuff pressure began to drop 100 msec after the occurrence of the R wave. About 2/3 of the final negative pressure was achieved 180 msec later. The negative pressure remained for an interval which lasted as long as half of the previously recorded mean interbeat interval minus 100 msec. Then a positive cuff pressure was applied for exactly the same duration. The valves were then opened and atmospheric pressure persisted until the next R wave was detected. The entire sequence repeated, resulting in a continual wave of bipolar pressure pulses. In the present experiment, this continual wave was presented for periods of 6 sec each. Within the 6 sec period, a train of 4–9 (depending on the particular heart rate) sequences of positive and negative cuff pressures was presented.

For systolic pressure/diastolic suction trials, the sequence of negative and positive pressure pulses was reversed in time: each R wave triggered a positive cuff pressure (again for 50% of the time of the previously recorded mean minus 100 msec). This period was followed by a pressure pulse of equal duration. If the next R wave occurred prior to the completion of the bipolar

pressure pulse, 100 msec later the current pulse was interrupted and the next one was initiated. During suction periods, a negative pressure of approximately 30 mm Hg was applied; the positive pressure was of the order of 10 mm Hg. This asymmetry is due to the cuff forming a tighter seal during suction than during positive pressure. As noted in Rau et al. (1992), minor variations in these pressure values have no significant effect on baroreceptor activation, which is achieved through the special timing features of PRES. As a result, the absolute values of pressure are not recorded.

To prevent subjects from discriminating between the two conditions, each trial began with a negative pressure burst. If an R wave occurred before the sequence of pressure changes had been completed, the new sequence was initiated.

Fig. 1 elucidates both the positioning of the cuff and the experimental protocol.

Tendon reflex measurement

T reflexes were evoked in the right leg by means of a 5 cm long by 2 cm diameter plastic rod which hit the Achilles tendon, the angle between the rod and the tendon being perpendicular. The rod had a flattened curvature at the side where it hit the tendon. It was mounted on a piston, resulting in a T-shaped hammer, with the trunk of the T being the piston and the vertical line being the rod. The fixation of both the leg and the stimulator guaranteed that the hammer always hit at the same place at a right angle, force and velocity being constant for every stimulation. The force was

Fig. 1. The position of the cuff on the subject is depicted in the upper left corner. A schematic representation of the experimental protocol is depicted. Following a 1 sec baseline, 1 of the 4 depicted conditions is pseudo-randomly initiated. The wave forms represent changes in cuff pressure, the arrows indicate the timing of ECG R waves, and the hammer symbol depicts the timing of reflex elicitation. Following a trial, there is a 1 sec post-baseline, and a 13–23 sec intertrial interval, following which the process is repeated until 16 trials of each of the 4 conditions have been performed.

individually adjusted to provoke a visible reflex response. It was mounted on a vibration excitor (Brüel and Kjaer) which was triggered by a 9 msec half wave, produced by a Brüel and Kjaer 2706 power amplifier.

Physiological recording

The ECG was recorded from Ag/AgCl electrodes attached to both sides of the lower rib cage. The raw ECG was fed into a cardiometer module (Beckman) for R wave detection. Heart rate was calculated from the R-R intervals and stored on hard disc. The EMG was obtained from Ag/AgCl surface electrodes attached 4 cm apart on the distal part of the right soleus muscle. The signal was amplified by a Hellige EE preamplifier (bandwidth 0.3–750 Hz, roll-off –3 dB/octave) and sampled at a rate of 1 kHz. In addition, a rectified EMG was obtained from two adjacent electrodes, amplified through a Beckman type 9852A coupler and also digitized continuously at the same sampling rate. This second EMG channel served only to control for variations in tonic EMG.

Data analysis

For each subject rectified EMG and heart rate responses were averaged separately for the 4 trial categories.

The means of the heart rate during the last half of each trial (seconds 4–6) and the averages of the recti-

fied EMG during second 6 were submitted to an ANOVA with the within-subjects factor PRES (baroreceptor activation or control).

T reflex amplitudes were scored as the difference between the maximal and the minimal raw EMG in a latency window from 30 to 80 msec after the trigger pulse to the Brüel and Kjaer device. These peak-to-peak measures were averaged across trials but separated for the 4 different trial categories and for the 2 reflex elicitations during a trial. They were then transformed to *z* scores, defined as the difference between the mean of each trial category and the mean of all trials divided by the standard deviation computed over all trials of that particular subject. These *z* scores were submitted to an ANOVA comprising the 3 within-subjects factors, each with 2 levels: PRES, CARDIAC PHASE (elicitation of T reflex during systole or during diastole) and ELICITATION (first vs. second T reflex elicitation in a trial).

Results

Heart rate

In all subjects, baroreceptor activation (the sequence systolic suction/diastolic pressure) evoked a greater heart rate deceleration than did the systolic pressure/diastolic suction condition. Fig. 2 depicts 4

Fig. 2. Heart rate responses for 4 subjects, averaged separately for the two PRES conditions. The manipulations (R wave triggered changes in cuff pressure) started at time 0 and ended with second 6. For illustration purposes 4 subjects were selected: those with the largest and those with the smallest response differentiations in the heart rate and in the T reflex amplitudes. Thin line: diastolic suction/systolic pressure. Thick line: systolic suction/diastolic pressure.

Fig. 3. EMG responses to Achilles tendon reflex elicitation, averaged separately for elicitations during systole under systolic suction (thick line) and during diastole under diastolic pressure (thin line). In every case, the latter had equal or more extreme peaks and troughs. The same 4 subjects are displayed as in Fig. 2.

single subject responses (averaged over trials) of the heart rate for both conditions. The difference between conditions is confirmed by a significant effect of the factor PRES $F(1, 11) = 41.5$, $P < 0.001$.

EMG

The tonic EMG levels extracted from the rectified EMG channel were low and did not differ between conditions.

Fig. 3 illustrates 4 subjects' mean Achilles tendon reflexes elicited in the EMG of the soleus muscle. The amplitudes of these T reflexes varied systematically depending on the particular condition. The ANOVA yielded a significant main effect of CARDIAC PHASE, $F(1, 11) = 8.0$, $P < 0.02$ and an interaction of CARDIAC PHASE $\times$ PRES $F(1, 11) = 24.9$, $P < 0.001$. In order to estimate the magnitude of the effect, we compared the conditions having minimum and maximum baroreceptor activity (T reflex with systolic suction/diastolic pressure, elicited during systole versus diastole). The percentage change, referred to the individual mean reflex amplitude, averaged -14.9 (S.D. = 12.8), and ranged from -1.0 to -46.6 .

This interaction is plotted for the averaged z scores, together with 1 S.D. confidence limits in Fig. 4. Post hoc contrasts indicated that there were significant differences between systolic and diastolic reflex elicitation during systolic suction ($F = 37.0$, $P < 0.0001$), between

systolic and diastolic suction for diastolic reflex elicitation ($F = 21.1$, $P < 0.001$), between systolic suction with diastolic reflex elicitation and diastolic suction with systolic reflex elicitation ($F = 13.1$, $P < 0.01$), and for systolic reflex elicitation between systolic and diastolic

Fig. 4. Interaction between CARDIAC PHASE (the time of reflex elicitation in the cardiac cycle) and PRES (systolic suction/diastolic pressure vs. diastolic suction/systolic pressure) for the averaged z scores of Achilles reflex amplitude, with 1 S.D. error bars. The plot shows that under conditions of maximal stress of the arterial walls, there was a disfacilitation of the tendon reflex, while the reflex was largest during minimal stretch.

suction ($F = 6.1$, $P < 0.05$). The superposition of the internal pulse wave with the external suction pulse damps the T reflex while positive pressure produces the largest amplitudes when the reflex is evoked during the diastole. Thus, the smallest amplitudes were obtained when the stretch of the arterial walls in the carotid sinus region and its rate of change were largest. During diastole, the internal pressure was relatively low and a positive pressure pulse reduced the stress of the arterial walls even more, resulting in the largest T reflex.

There was a non-significant trend ($F(1, 11) = 3.0$, $p = 0.11$) for the second reflex in a trial to produce somewhat weaker results.

Discussion

The present results are consistent with the assumption that increased carotid baroreceptor activity reduces nervous excitability at the spinal level. If an external suction pulse was applied to the carotid baroreceptors simultaneously with the internal pulse wave, the Achilles tendon reflex became significantly smaller than baseline while the opposite condition (i.e., an excess pressure during diastole) generated reflex amplitudes larger than baseline.

The decrease in T reflex amplitude can be due to an inhibition or a disfacilitation of alpha motoneurons or of interneurons impinging upon them. Since only Achilles T reflexes were investigated, it is unclear whether this inhibitory effect is a result of a generalized process or not. Other reflexes at the same or at different segmental levels need to be investigated to elucidate this problem further. Moreover, it is unclear whether the descending influences are based upon a postsynaptic or presynaptic inhibition. The latter is difficult to demonstrate directly, but Hultborn et al. (1987a,b) have presented convincing evidence for it (Rudomin 1990).

The increase in T reflex amplitude is presumably based upon the reverse process, that is, a decrease in inhibition, or an increase in facilitation of the alpha motoneurons in a direct or indirect way, or a release of presynaptic inhibition.

In addition to the descending effects, deactivating ascending effects have been reported. Cortical excitability can be modulated through baroreceptor input, resulting in reduced nociceptive sensitivity (summarized in Elbert and Rau 1993; Rau et al. 1993b) and positivity shifts in slow brain potentials (Elbert et al. 1988; Rau et al. 1993a,b). Although it remains somewhat uncertain as to how these extrahomeostatic effects are realized, it is likely that the observed effects are largely generated via one and the same influence of the baroreceptors on the reticular activating system

(Magnes et al. 1961; Bonvallet and Allen 1963). Possibly, solitary tract neurons inhibit neurons in the reticular formation. The changes during baroreceptor activation, observed for the ascending as well as for the descending pathways (spinal reflex), have some similarities with observations during states of drowsiness and even sleep. Stimulation of pressure receptors enhances EEG theta activity (Vaitl and Gruppe 1991, 1992) while the upright posture inhibits sleep by reducing baroreceptor firing (Cole 1989). A reduction of spinal reflex amplitudes is generally observed during sleep (Hodes and Dement 1964).

Brunia (1979) used propranolol to investigate the sympathetic influence on muscle spindles. Compared to rest periods before and after mental arithmetic, heart rate and T reflex amplitude increased during the task in subjects under placebo. The β -adrenergic blocker blocked the cardiovascular response and disinhibited the T reflex during the task, a result which can be interpreted as possibly resulting from a reduced baroreceptor load under the β -blocker compared to the placebo condition. The stressful task has facilitatory influences on the spinal motoneurons, which in placebo subjects is counteracted by enhanced baroreceptor activity mediated through an increase in sympathetic arousal. If the latter response is blocked, baroreceptor activity will change to a lesser degree and the facilitatory influences may become larger. In a similar paradigm, Schweizer et al. (1991) found that propranolol exacerbated self-reported stress levels during mental arithmetic.

Integrating both cardiovascular and central nervous effects of baroreceptor activation, one could speculate that PRES induced heart rate deceleration leads to reflex inhibition. However, the results of the propranolol study (Brunia 1979) indicate that heart rate decrease can be accompanied by reflex increases.

The cumulative research on the influences of baroreceptor activity on pain, EEG slow waves, EEG power spectra, gross measures of arousal (sleep) and monosynaptic reflexes suggest that baroreceptor activation has a generalized damping effect on the central nervous system.

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