THE FUNCTIONAL ORGANIZATION OF THE DESCENDING INFLUENCES IN THE NON-PROJECTION CORTICOOTHALAMIC SYSTEMS OF THE CAT BRAIN

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Key words: non-projection corticothalamic systems, polysensory cortical areas, association thalamic nuclei, modal-specific corticofugal influences

Abstract. The local cooling of parietal, frontal or motor cortical areas in cats under Nembutal anesthesia changed evoked potentials (EPs) in pulvinar, lateral posterior and medial dorsal thalamic nuclei. Parietal cortex, cooling led to rapid and significant changes of visual EP and delayed but strong changes of somatic EP in the pulvinar-lateral posterior complex. In contrast, frontal cortex cooling led to fast changes of somatic EP in medial dorsal nucleus and caused delayed weak changes of visual EP. Motor cortex cooling resulted in rapid transformations of both potentials, though the changes of somatic EP were more pronounced in medial dorsal nucleus. The modifications of both EP primary and secondary components were modal- and system-dependent. Results suggest that polysensory cortical areas exert modal-specific corticofugal influences on signals of different modality or on signals of the same modality but different subcortical genesis in the association nuclei.

INTRODUCTION

The non-projection polysensory areas of the cortex, as a locus of an intense convergence and integration of heterogenous signals, play an important role in the systemic activity of the brain (1–5, 10, 12, 22, 31). The polysensory areas vary in their morphological and functional organization, forming a definite hierarchy of cortical structures (1, 2, 9, 24).
Accordingly, Adrianov (1, 2) classified them into the association (frontal and parietal) and the integrative-trigger (orbital and motor) areas. The latter designation describes the close overlapping of the afferent polysensory projections with the efferent ones which descend into the pyramidal tract.

The polysensory non-projection cortical areas of the cat are bilaterally connected with a number of cerebral structures (9, 10, 15, 17, 20, 28). Thus each polysensory area receives the local volleys from its activating structures and regulates the afferent volleys at the level of these structures, including the thalamus. These interrelations underlie the distinct thalamo-cortico-thalamic non-projection systems of the brain, similar to the projection systems represented by the respective sensory projection areas in the cortex and by the relay nuclei in the thalamus. Several lines of evidence demonstrate the existence of the association thalamo-parietal, thalamo-frontal (3, 6, 8, 9), as well as parieto-thalamic and fronto-thalamic non-projection system (2). Due to bilateral connections of the motor cortex with the subcortical structures activating it (1, 10, 24, 30), in addition to the mentioned non-projection systems, we distinguish also the thalamo-cortical and the cortico-thalamic integrative-trigger systems, represented by the motor area in the cortex and by several structures in the thalamus including the association nuclei.

The question how the cortical structures of the mentioned non-projection systems influence the diverse afferent signals arriving at the thalamic nuclei is not yet solved. The aim of the present investigation was therefore to study the character of the corticofugal action of the cat’s non-projection cortical areas on the heterogenous volleys in the respective thalamic association nuclei. We studied the descending influences on the association nuclei as follows: in the association parieto-thalamic system — on the pulvinar (Pul) and lateral posterior nucleus (LP) forming a single complex (13, 18, 19); in the association fronto-thalamic system — on the medial dorsal nucleus (MD); in the integrative-trigger (motor) system — also on the MD of the thalamus.

METHODS

Experimental observations were made under Nembutal anesthesia (30–40 mg/kg) on 68 adult weighing 2.5–3.5 kg. In each animal we locally cooled different cortical areas, or repeatedly the same area. In all, 160 observations were recorded, which were divided into 4 series (40 observations in each series) in the following way: (i) cooling of the parietal cortical area while recording evoked potentials (EPs) in LP; (ii) cooling of
the parietal cortical area while recording EP in Pul; (iii) cooling of the frontal cortical area while recording EP in MD; (iv) cooling of the motor cortical area while recording EP in MD.

Monopolar recordings were used with the reference electrode placed on the bone of the frontal sinus. Steel electrodes with a tip diameter of 30–60 μm were used for EP recordings. Recording electrodes were inserted according to stereotaxic coordinates by Jasper and Aymone-Marsan (16). LP: +7–7.5; L 4–5.5; H +3–4; Pul: A +6–6.5; L 5.5–7; H +5–6; MD: A +8–8.5; L 1–2; H +2–3. Electrode positions in association nuclei were verified on histological preparations. The somatic and visual EPs in Pul and LP were compared to the responses in the ventrobasal complex of the thalamus which served as the electrophysiological control of the electrode position.

Single somatic and visual stimuli were applied contralaterally: rectangular current shocks were applied (10 V, 0.5 ms) to the brachial plexus nerves and diffuse light flashes (0.3 J, 0.05 ms) — to the atropinized eye. The somatic and visual stimuli were presented in turns with intervals of 15–30 s. This enabled us to compare the characteristic changes of the EP recorded using stimuli of different modality in the process of cooling in identical experimental conditions. EPs were photographed single frame with subsequent superposition of 5 traces.

The exposed cortex was covered with warm vaseline (37°C) which was removed from the places undergoing cooling. Each neocortical area was locally cooled by ice in a rubber container. The temperature of the cooled area was maintained at 19–20°C, returning to normal at the depth of 3–3.5 mm and with a radius of 2.5–3 mm on the surface of the cortex. Chromel-capel thermocouple was used to measure temperature shifts. The cortex was cooled for 30 min, then warmed up along with the registration of EPs in the appropriate association nucleus until a complete EPs recovery to the initial (control) level.

RESULTS

The parieto-thalamic association system

Single light flashes under Nembutal anesthesia regularly produced complex visual EPs in LP and Pul of the thalamus. The primary component of these EPs is composed of positive and negative waves (Fig. 1A, 1,7; C, 1,7), the secondary component is represented by a positive waves (Fig. 1A, 1, 7), or also by a positive-negative oscillation (Fig. 1C, 1, 7). The effects of parietal cooling on visual EP in LP and Pul was determined by changes of both phases of the primary component and the subsequent positive wave of the secondary EP component.
Fig. 1. The effect of parietal cooling on the visual evoked potentials (EP) in lateral posterior nucleus (LP) and pulvinar (Pul). A and C, traces of EP recording in LP and Pul respectively: 1, prior to cooling; 2–6, during cooling; 7, after restoration of normal cortical temperature. The digits placed over the frames show the time count from the onset of cooling. B and D, the amplitude plots of single EP waves recorded in LP and Pul respectively versus the time of cortical cooling. On the abscissa—the time elapsed from the onset of cooling. On the axis of ordinates—points of the percent values of the average amplitude obtained in the process of cooling with respect to the initial values. P_s, the positive wave of the primary EP component; N_s, the negative wave of the primary component; P_n the positive wave of the secondary EP component; N_n the new negative wave replacing P_n.
Local parietal cooling (anterior part of the gyrus lateralis, anterior and medial parts of the gyrus suprasylvius) resulted in a rapid and pronounced modification of visual EP in LP (Fig. 1A; B). These changes started 15–30 s after the onset of cooling (Fig. 1A, 2). The visual EP components decreased during the 1st and 2nd min of cooling. The average decrease of visual EP primary component in LP was 12% in the 1st min, and 30% in the 2nd min vs. 46% and 70% respective values for the secondary positive wave (Fig. 1B).

Still more pronounced modifications of the components of visual EP in LP were observed between the 3rd and 5th min of parietal cooling. The secondary positive deflection completely vanished (Fig. 1A, 3; B), to be replaced by a new negative wave after an interval of time (Fig. 1A, 4; B). It appeared immediately after the negative phase of the primary visual EP component and persisted up to the end of the parietal cooling (Fig. 1A, 5, 6; B). As to the visual EP primary component, in LP, both its phases were preserved, but essentially decreased in amplitude during the first 12 min of cooling: postive wave — 52% on the average, ne-
gative — 82% (Fig. 1A, 3–6; B). Further parietal cooling (up to the 30th min) produced no noticeable changes of visual EP in LP.

Changes of the primary and secondary components of visual EP were also recorded in Pul during parietal cooling (Fig. 1C, D). A 10–20% increase of visual EP amplitude could be observed during the first 1.5 min of cooling (Fig. 1C, 2; D). However, this did not affect the general character of the subsequent transformation of visual EP in Pul, which corresponded to the changes of the primary and secondary components of visual EP in LP (see Fig. 1A, 3–6 and C, 3–6; B and D).

Besides visual EP, somatic EP were recorded in Pul or LP upon electric stimulation of brachial plexus nerves. The amplitude and time course of visual and somatic EPs differed although they were registered using the same electrode (Figs. 1 and 2). Under Nembutal anesthesia somatic EP were often represented only by the secondary component, consisting of the positive and negative waves (Fig. 2A, 1, 4; B,1, 4). The secondary component was irregularly preceded by an initial negative wave (Fig. 2B, 1, 4) or positive-negative wave complex of varying form and latency, sometimes difficult to be distinguished in the EEG background.

Clear changes of somatic EP in Pul and LP were also observed during local parietal cortex cooling. Special attention is given to the late occurrence of these somatic EP transformations in Pul and LP. A clear tendency to the decrease of its secondary component could be noticed only in the 8th min on the average (Fig. 2A, 2; B, 2; C). Further, its transformation proceeded intensively, reaching the maximum near the 12th min of cooling. At this final stage somatic EP either sharply diminished (by 90% on the average) (Fig. 2B, 3; C, 1) or vanished completely in the EEG background (Fig. 2A; 3; C, 2). The changes of the initial somatic EP component (if present) were similar to those of the secondary waves (Fig. 2B, 3). The changes of both components of somatic EP were very similar in LP, Pul.

Thus the cooling of the cortical area in the parieto-thalamic system provoked different changes of visual and somatic EPs recorded from one and the same point of Pul or LP. At the same time the changes of the components of both visual and somatic EPs were very similar in Pul and LP, that is, these nuclei showed the same type of reaction during parietal cooling. Thus these nuclei operated as a single complex not only when processing the ascending afferent signals, which gives them the name of “pulvinar-lateral posterior complex” (Pul-LP complex) in References (13, 18, 19), but also, in agreement with our data, when processing the descending (corticofugal) volleys.
The fronto-thalamic association system

The visual and somatic EPs at the same points of the thalamus under Nembutal anesthesia had a different amplitude and time course (Fig. 3A, 1, 7; 4, A, 1, 7). The visual EP primary component in MD consisted of a positive and negative phase. In some cases its configuration was even more complicated, comprising a three-phase negative-positive-negative oscillation. The visual EP secondary component consisted of a positive-negative wave. The same components of the same configuration as in visual EP in MD were regularly present in somatic EP of MD. It was therefore possible to compare visual and somatic EP changes in MD during frontal cooling using the same indicators. We used the primary component, in case it was presented by the two phases of wave and the positive deflection of the secondary component in both kinds of potentials (Figs 3A, 1 and 4A, 1).

Local frontal cortex cooling (lateral part of the gyrus proreus) chan-

![Fig. 3. The effect of frontal cooling on the somatic evoked potentials (EPs) in medial dorsal nucleus (MD). A, traces of EP recorded in MD during cooling. B, the amplitude plot of single EP waves versus the time of cooling. See Fig. 1 for details.](image-url)
ged somatic EP in MD. The transformations started already 12–15 s after the onset of cooling and could be clearly traced during the first 12 min of cooling (Fig. 3A, 2–6; B). As to the time course and type, somatic EP transformations in MD were similar to those of the visual EP in the Pul-LP complex during parietal cooling (Figs. 1 and 3). The distinctions consisted of certain nonidentical changes of absolute values of the responses.

The decrease of the somatic EP primary component was 16% and secondary component — 21% on the average during the 1st min of frontal cooling (Fig. 3A, 2; B). In the middle of the 2nd min these modifications were 33% and 70% respectively (Fig. 3A, 3; B). Further gradual decrease of the primary positive and primary negative components of somatic EP comprised on the average 68% and 87% respectively (Fig. 3A, 4–6; B). The secondary positive oscillation disappeared (Fig. 3A, 4; B) and instead of it a new negative wave appeared (Fig. 3A, 5, 6; B).

Fig. 4. The effect of frontal cooling on the visual evoked potentials (EPs) in the medial dorsal nucleus (MD): A, traces of EP recorded in MD: 1, prior to cooling; 2 and 3, during cooling; 4, after restoration of cortical temperature. B, the amplitude plot of single EP waves versus the time of cooling. See Fig. 1 for details.
Frontal cooling resulted in a quite contrasting effect on visual EP in MD. No definite tendencies in transformations could be observed until the 4th min of frontal cooling. The visual EP changes which appeared at that time were relatively small and concerned only the primary component (Fig. 4A, 2 and B). Its amplitude decreased by 12% on the average, remaining constant during further stages of cooling, including the period when somatic EP were still undergoing considerable changes (Figs. 3A, 5, 6; 3, B and 4, A, B).

Thus, frontal cortex cooling elicited highly contrasting changes of visual and somatic EPs in MD of the thalamus, as was the case with visual and somatic EPs in Pul-LP complex during parietal cooling. The main features and the time course of the compared EP changes in parieto-thalamic and fronto-thalamic systems were nevertheless different. During parietal cooling visual EP underwent rapid and intense transformations in Pul-LP complex, whereas somatic EP changes occurred much later. In contrast, frontal cooling resulted in rapid and pronounced transformations of somatic EP as opposed to the more delayed and slight changes of visual EP. In addition, the transformations of single EP components were unsimilar.

The integrative-trigger (motor) system

As we mentioned above, this corticothalamic system is represented in the cortex by the motor area (the gyrus sigmoideus anterior and the extreme anterior part of the gyrus sigmoideus posterior). Changes of somatic and visual EPs in MD during motor cortex cooling were identified using the same indicators as in the case of frontal cooling: changes of the two positive-negative phases of the primary component and of the positive wave of the secondary component (Figs. 5A, 1, 8 and 6A, 1, 8).

A complex time course is characteristic for transformations of somatic EP in MD. It is clearly seen in Fig. 5. EP transformations started rapidly (15–30 s). In the 1st min of motor cooling both the positive and negative waves of the primary component decreased by about 50%, while the secondary component positive wave decreased by about 70% (Fig. 5B). Around the middle of the 2nd min the latter was out of notice (Fig. 5A, 2; B). Instead a new negative wave appeared and was also recorded in the 3rd or 4th min (Fig. 5A, 3; B). At this time both waves of the somatic EP primary component decreased on the average by 75%. However, by the 5th min both waves of the primary component increased sharply, the new negative wave disappeared and the secondary positive oscillation reappeared again (Fig. 5B). In the 6th min both somatic EP components grew up to and exceeded the control level by 16% on the
average (Fig. 5A, 4; B). Such transformations of somatic EP, including the aperiodic sequences of amplitude increase (which might exceed or not exceed the control level) and decrease (which might be accompanied by transformations in response structure) took place during the whole process (30 min) of motor cooling (Fig. 5A, 2-7; B). The primary component and the secondary positive wave of somatic EP usually increased above the control level by 12–20% or decreased by 65–75%, demonstrating considerable amplitude variations and aperiodic mode of amplitude changes both in the same experiment (Fig. 5B) and in different experiments.
During motor cortex cooling visual EP in MD did not undergo such complex changes as somatic EP (Figs. 5 and 6). Following 15–30 s of cooling, there was rather a small decrease of visual EP as compared to the control level (Fig. 6 B). The unidirectional visual EP transformations were observed both in the primary and the secondary components, whole...

![Fig. 6. The effects of motor cooling on the visual evoked potentials (EP) in medial dorsal nucleus (MD). A, traces of EP recorded in MD: 1, prior to cooling; 2–7, during cooling; 8, after restoration of cortical temperature. B, the amplitude plot of single EP waves vs. the time of cooling. On the axis of ordinates — the average amplitudes of single EP waves. See Figs. 1 and 5 for details.](image)

decreasing amplitude fluctuated at the new level (Fig. 6A, B). During the first 10–15 min of cooling the EP primary component decreased on the average by 15% and the secondary component — on the average by 23% (Fig. 6A, 2–4; B). Later on (up to 30 min) the primary component decreased by 30% and the secondary component — by 44% on the average (Fig. 6A, 5–7; B).

Thus, motor cortex cooling elicited sharp differences in changes of visual and somatic responses. Moreover, while the changes of the primary and secondary components of somatic EP might differ, those of visual...
EP were similar (Figs. 5 and 6). Besides, the transformations of somatic and visual EPs in MD were quite different during motor or frontal cooling. Frontal cortex cooling elicited a monotonous gradual decrease of somatic EP combined with a reconfiguration of these responses and a lack of both somatic EP components increase, as in the case of motor cooling (Figs. 3 and 5). The amplitude decrease of visual EP during motor or frontal cortex cooling was also not uniform though in one direction. Frontal cortex cooling, unlike the motor one, displayed only a relatively late and small decrease of the visual EP primary component and a lack of amplitude fluctuations at the new level (Figs. 4 and 6).

DISCUSSION

Our results show that cortical areas of both the association and the integrative-trigger (motor) non-projection systems exert highly differentiated descending influences on the heterogenous signals in the corresponding association thalamic nuclei. This is evidenced by the strong different changes of visual and somatic EPs recorded in identical points of the Pul-LP complex during local parietal cortex cooling, or in MD during local frontal or motor cortex cooling. We consider as modalspecific the said differentiated influences from the polysensory non-projection areas on the multivalent volleys in the association nuclei.

In each non-projection system there is a nonuniform type of modalspecific cortical influences on the valleys of various sensory quality in the corresponding nuclei. The observed rapid occurrence (15–30 s) of the initial changes of visual EP in the Pul-LP complex following the onset of parietal cortex cooling, somatic EP in MD or both kinds of EPs in MD following the onset of frontal or motor cortex cooling respectively, when the amplitude of responses in the cooled cortical zone itself decreases acutely (24, 26), suggests, that non-projection areas influence directly the signals producing these responses. This conclusion is consistent with the data showing the existence of well developed direct bilateral connections of the parietal cortex with the Pul-LP complex (13, 14, 17, 24), while the frontal and the motor areas have bilateral connections with MD (1, 8–10, 29). Delayed to a greater extent modifications of EPs recorded in the same nuclei using stimuli of another modality suggest that there is an indirect effect from the polysensory areas upon the volleys producing these EPs.

Thus, in spite of the existence of close direct morphological connections between thalamic and the corresponding cortical structures, the latter may influence not only directly, but indirectly the ascending volleys in the association nuclei; according to our data (25, 26) this
action comes along on polysynaptic round-about way acting not at the level of these nuclei but in the reticular formation of the midbrain. Thus, the parietal cortex directly affects visual signals in the Pul-LP complex, and indirectly — the somatic ones. In contrast, the frontal cortex directly affects the somatic volleys in MD, and indirectly — the visual ones. The motor cortex directly affects both kinds of impulses.

This data suggest that the modal-specific corticofugal action in the non-projection systems is realized thanks to the partition of their descending pathways into separate subsystems. Different transformations of single components of visual and somatic EPs in the nuclei during cooling make us think that there is a subtle subdivision of the corticofugal pathways into separate subsystems, which transmit the descending actions from the cortical areas to signals of the same modality but differing subcortical origin in association nuclei.

While discussing this problem one must bear in mind that the multimodal ascending volleys form separately functioning neuronal populations in the association nuclei (4, 6, 7, 18). Our data (25–27) showed that signals producing primary and secondary components of visual and somatic EPs in the Pul-LP complex and MD are also formed by separately functioning neuronal populations in these nuclei. The close connections of afferent and efferent (corticofugal) collaterals have also been shown in the association nuclei (29). All this data lead us to suppose that the descending modal-specific action from the non-projection areas to the heterogenous impulses in “their own” association nuclei is realized due to the selective connection of each corticofugal subsystem with the neuronal population activated by the ascending volleys of certain genesis.

We should note in addition that the functional specificity of the association nuclei studied here is of certain importance in the formation of these interconnections in the non-projection systems. The Pul-LP complex serves as a main station in the thalamus for direct transmitting of visual impulses to the parietal cortex and as an indirect link conveying the somatic volleys to it (11, 13, 26). MD plays an important role in the conduction of somatic afferent signals into the frontal and motor areas (1, 8, 9, 21, 27). The descending action of non-projection areas on the heterogenous impulses in “their own” association nuclei is organized on similar principles, as is evidenced by the modifications of subcortical EPs during parietal cortex cooling, which strongly and directly influences just the visual volleys in the Pul-LP complex and, as we mentioned above, acts upon the somatic volleys only indirectly. The influence of the frontal and motor areas in MD is far greater on the somatic impulses as compared to the weaker action on the visual afferent signals. Thus,
the principle of overlapping ascending and descending (corticofugal) projections in thalamic nuclei proved by morphological investigations (1, 17, 28), has been confirmed by our physiological experiments.

We should stress the differences in the organization of the corticofugal influences between the association and the integrative-trigger systems. The single components of subcortical EPs in the association systems undergo a gradual decrease or disappearance by the cooling of the respective cortical areas, and it suggests that the latter in intact animals has a facilitating-modulating or controlling influence on the realization of the heterogenous impulses in the nuclei. This influence is characterized by a tonic type of process. The appearance of the new negative wave during cooling is considered to be an electrographic sign of the enhanced activity of the nuclei themselves, released when the above cortical facilitating influences cease (23).

In contrast to these tonic facilitating influences, including the effect of the frontal cortex on MD, in the integrative-trigger system the motor cortex exerts a complex dynamic influence on MD — facilitating and inhibitory effects. This is inferred from the alternating increase and decrease of somatic EP in MD during motor cooling. The visual volleys in MD receive only a facilitating influence from the motor cortex, though of a different type from that of the frontal cortex (visual EP decrease differently during the cooling of these two areas). Besides, as we mentioned above, the motor area directly influences both signals in MD, while the frontal area influences immediately only somatic signals in that nucleus, acting upon the visual signals indirectly.

Thus, MD functions differently in the association fronto-thalamic and in the integrative-trigger systems. This, in turn, enables us to conclude that the corticofugal influences from the various polysensory areas are not only modal-specific, but are characterized by subtle functional specialization defining the nonsimilar activity of one and the same nucleus as it contributes to different systems. Such specialized corticofugal control over the activity of the association nuclei is characteristic of all polysensory area, and this may be traced in the nonsimilar changes of the EPs recorded using stimuli of the same modality in the respective nuclei during local cooling of various areas of the cortex.

In conclusion, it must be emphasized that the described characteristics of the functional organization of descending influences in the non-projection corticothalamic systems ensure the preservation of the modal and the functional specificity of the signals supplied by the polysensory areas to the related association thalamic nuclei, similarly to the way the cortical areas in the projection systems influence the corresponding thalamic relay nuclei.
REFERENCES


Accepted 4 October 1984