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Motion speed and reaction time after section of the pyramidal tracts in cats

Discussion of M. Wiesendanger's paper

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An essential result of the studies WIESENDANGER has presented is that pyramidal section produces only minor motor deficits. After a week the cats move about, climb and play as though nothing had happened to them. Early investigators were surprised to find this lack of motor deficit after section of the motor tract par excellence but the matter has been in dispute since SARAH TOWER in 1935 reported serious and permanent functional loss in extremities contralateral to pyramidal section. The only plausible explanation why TOWER alone found such serious symptoms is that her lesions were larger. The medial lemniscus was involved, possibly also the reticular formation of the medulla oblongata, directly or by gliosis surrounding the surgical lesion.

As a consequence of his results WIESENDANGER has wisely shifted his attention to other possible aspects of pyramidal function and his elegant study of the effect on sensory transmission followed a hint given by recent anatomical investigations. The more subtle aspects of the play of the pyramidal tract upon the neurons of the dorsal horn is an exciting field for future investigation. PAT WALL at M. I. T. has evidence that impulses descending from the brain may, in fact, change the modality of dorsal horn neurons.

For the rest of this brief presentation I shall propose the thesis that the pyramidal tract, in addition to its influence on sensory transmission, may have a direct motor function which may be highly significant to the animal and the species although it is not obvious to general observation. I had the pleasure of having Dr. WIESENDANGER as a partner in the investigation on which I base my view.

We studied motor speed by training cats to repeat a simple movement, that of pressing a lever 30 times to get each of the 80 to a 100 little bits of food which was the cat's daily food ration. Each response raises the line of the graph by a small step and the slope of the curve therefore indicates response rate. On this training schedule a cat performed at a rate of 2 responses/sec before the operation and she performed about 2300 responses in 25 minutes without showing any fatigue – the response rate stayed at 2/sec. 18 days after a pyramidal lesion was made, which interrupted 60–70% of each pyramid, the cat ate, drank moved about and pressed the lever in the training box as a normal cat and her initial response rate in a day's session was as high as before the operation. The difference is that the response rate declined during the session and pauses appeared and the average response rate for the whole session was reduced. Now, what does this mean? Was the cat slowed? No, because she performed hundreds of responses in succession at the same rate as before the operation. Was she less hungry? Not in any simple way at least because she went on to take as many bits of food as before the operation. Did she become tired? At first sight this may be an appropriate description but there was no gradual slowing leading to a pause and no pick up in response rate after the pause as might be expected if fatigue were responsible for the change. Whatever the explanation, the cat was able to repeat a simple movement at the same rate before and after a pyramidal lesion.

Next we investigated the same lever pressing movement in a more complex context; we deviced a task in which cortico-spinal activity was likely to play a role. In the training box there were two lights, two levers and a platform to step on. Stepping on the platform lit the two stimulus lights with different brightness and the cat was trained to press the lever under the brightest light to obtain a bit of food. About a hundred responses were emitted in a day's session and towards the end of training only 10% were on the lever under the weakest light. These incorrect responses were punished mildly in that they made the machine inoperative for 20 sec. That is a long time for a hungry cat. The feeder was set aside in a separate compartment of the training box so that the cat had a standardized route of approach to the stimuli and levers. We measured the response latency, defined as the time from when the platform was depressed to when the lever press response was performed and the results are displayed as a latency histogram. We trained the cats until their performance was stable, stability being less than a $\frac{1}{4}$ sec change of the median of the latency distribution, and more than 80% correct responses for 10 days in succession.

Apparently some cats did not respond as quickly as they could, when they could choose their own pace. The cat was trained for 4 days with the special contingency of no food reward for correct response with latencies longer than 1.5 sec. After a lesion was made in the pyramids the cat worked again after a brief recovery period but she did not meet the stability criteria until 3 months lather. Some sort of recovery of function is presumably represented by her gradual approach to stable performance during the 3 months. In this investigation we did not use the data until the process was completed and performance was stable. The spontaneous latency distribution was only slightly different from the preoperative distribution. Selective reinforcement of short latencies, however, had no effect; she could no longer be forced to respond faster.

Among the 8 cats on discrimination training 3 apparently responded as quickly as they could without special training for fast responding. Slowing in such a cat shows in the spontaneous latency distribution. Selective reinforcement of short latencies had no effect either before or after the operation.

Trying to explain that the cats in performing this visual discrimination problem were really slowed down we may again examine whether reduced hunger may be the cause. And again the cats took as many bits of food after the operation as they did before, neither did fatigue seem to be the reason for the shift in the latency distribution. In normal cats response latencies are slightly longer at the end of a day's session and the difference between end and beginning was the same in operated cats.

All the lesions in this investigation were incomplete because, to exclude damage by gliosis, we left intact tissue between the surgical lesion on the one hand and the medial lemniscus and the reticular formation on the other. The slowing in responding to a visual discrimination problem occurred after lesions interrupting more than half of one or both pyramids. It is interesting to note that a cat with a 50% unilateral lesion solely responded with the contralateral paw before as well as after the operation. Unilateral lesions involving 10% of a pyramid did not produce a deficit detectable by the method we used. These cats serve therefore as controls for unspecific effects of surgery.

Finally we must discuss whether the effect on response latencies was specific of pyramidal lesions. Buser and Rougeul (1961) have shown that ablation of the sensorimotor cortex increases the mean response latency of cats trained to press a lever to get food when clicks or flashes are presented. The operated cats were, however, handicapped by difficulties in executing the instrumental response by hyperactivity without purpose and episodes of disorientation and the response latencies were highly variable, some reaching 40 sec. The results of pyramidal lesions and of ablation of the sensori-motor cortex are obviously not the same.

We chose to make bilateral control lesions for specificity in the mesencephalon and the lesions involved the medial lemniscus to different extents. Slowing occured in a cat with about 50% involvement of the medial lemniscus on both sides: not in the two cats with less damage to the medial lemniscus. Damage to some other structure does not seem to be the factor determining whether or not slowing occurs. At this point we should have stopped the investigation. We went on to calculate the volume of the lesions in the three cats and found that the cat which was slowed and had the larger involvement of the medial lemniscus also had a total lesion about 35% larger than the two other cats. Consequently we cannot at this moment disprove that the slowing in a complex task is a completely unspecific effect – that it is produced by any 17 microliter hole in the brain of a cat. To decide whether response-latency measurements are at all worth doing we will plase lesions in unspecific thalamic nuclei.[1]

In conclusion we can say that pyramidal lesions produce slowing in a com-

[1] Note added in proof: Control lesions of twice the volume did not make the cat respond more slowly. Thus the effect of pyramidal and lemniscal lesions is not unspecific. The slowing produced by the lemniscal lesion is probably due to a reduced level of alertness (Sprague et al. Arch. ital. biol. 101, 225, 1963).

plex task: not in a simple repetitive one. The slowing is not specific because a cat with a medial leminiscus lesion was slowed.

Let us consider the significance of the slowing. As you saw it was very slight. Although clear enough summed up over 100 responses it was hardly detectable by simply observing the cats perform. At first sight a small decrease in response latency may seem a minor contribution of the pyramidal tract to the capacities of the nervous system. A cat solving the visual discrimination problem of detecting mice in darkness gets more mice, however, the faster she responds and fractions of seconds could easily make the difference between successful and unsuccessful cats. Thus the survival value of rapid responding in complex tasks may have contributed to the special development of the pyramidal tract in higher mammals.

Summary

Cats trained to press a lever 30 times to get each bit of a day's food ration pressed the lever at the same rate before and after damage to the bulbar pyramids. Response latency in a more complex task was increased after pyramidal as well as after lemniscal lesions. The complex task was a brightness discrimination where the two lights of different intensity were presented simultaneously; under each light was a lever and the cat was trained to obtain food after pressing the lever under the brightest light.

Zusammenfassung

Katzen, die darauf trainiert worden waren, einen Hebel dreißigmal herunterzudrücken, um jedesmal einen Bissen ihrer täglichen Futterration zu erhalten, taten dies vor und nach der Verletzung der bulbären Pyramide mit der gleichen Geschwindigkeit. Die Latenz der Reizbeantwortung bei der Lösung einer schwierigeren Aufgabe war sowohl nach der Verletzung der Pyramide als auch nach jener des Lemniscus verlängert. Die betreffende Aufgabe verlangte eine Helligkeitsunterscheidung, wobei die beiden unterschiedlich starken Lichter gleichzeitig aufleuchteten. Unter jedem Licht befand sich ein Hebel; die Katze war darauf trainiert, daß sie das Futter erhielt, wenn sie den Hebel drückte, der sich unter dem helleren der beiden Lichter befand.

Résumé

Des chats, entraînés à actionner un levier 30 fois pour obtenir une fraction de la ration journalière de nourriture, ont actionné le levier à la même cadence aussi bien avant qu'après une lésion des voies pyramidales du bulbe. Toutefois le temps de latence est augmenté lors d'un travail plus complexe aussi bien après la lésion des voies pyramidales que du lemniscus medialis. Ce travail complexe consistait en distinction d'intensités lumineuses diffé-

rentes, lorsque deux sources de lumière étaient présentées simultanément. Sous chaque source lumineuse se trouvait un levier que le chat était entraîné à actionner sous la lumière la plus intense pour obtenir de la nourriture.

Riassunto

Gatti allenati ad abassare una leva trenta volte per ottenere ogni volta un boccone del loro pasto quotidiano, eseguirono il loro compito con la stessa velocità sia prima che dopo lesione della piramide bulbare. Il tempo di latenza nel rispondere ad uno stimolo durante lo svolgimento di un compito difficile risultò prolungato tanto dopo lesione della piramide che dopo lesione del lemnisco. Il compito imposto richiedeva una distinzione di luminosità in quanto due luci di diversa intensità si accendevano contemporaneamente. Sotto ogni luce si trovava una leva; il gatto era allenato a ricevere il suo pasto quando abbassava la leva che si trovava sotto la luce più intensa.