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Displacement Activities and Arousal

IN 1940 Tinbergen[1] and Kortlandt[2] independently drew attention to a behavioural phenomenon which has since been called displacement activity and has received a good deal of attention[3,4]. Although no binding rules exist by which displacement behaviour can be recognized, the term is applied to behaviour patterns which appear to be out of context with the behaviour which closely precedes or follows them, either in the sense that they do not seem functionally integrated with the preceding or following behaviour or that they occur in situations in which causal factors usually responsible for them appear to be absent or at least weak compared with those determining the behavioural envelope. Displacement activities occur in three situations: motivational conflict, frustration of consummatory acts and physical thwarting of performance. Several theories have been put forward to explain the causal mechanism involved[5–8]. A variety of behaviour patterns have been reported as displacement activities[9], even in a single species, but this variety needs revision[10]. Monographic treatments of the behaviour of any one species usually indicate only two or three activities which according to the judgment of the observer occur commonly as displacement. None of the theories on displacement activities gives cogent reasons why particular behaviour patterns should be more common than others as displacement activities, apart from stating that the causal agents which usually elicit them in non-displacement situations can also be presumed to be present, if only weakly, in the displacement context, or remarking that these patterns are prepotent in the repertoire of the animal.

In the course of a systematic exploration of the forebrain and brainstem of herring and lesser black-backed gulls (*Larus argentatus* and *L. fuscus*) with electrical stimulation, information was obtained which may bear on this particular issue. The gulls with chronically implanted monopolar electrodes (conical active area $\sim 0{\cdot}25$ mm^2)[11,12] were stimulated with a sine current at 50 c/s ranging between 10 and 150 μamp root mean square current, in repeated trains lasting 30 sec–5 min for several testing sessions, over 2 or more months. The electrode tip locations were checked histologically.

A great variety of responses have been obtained, but here we will only consider a behavioural syndrome which is characterized by preening and staring down, and more rarely by pecking, yawning, squatting, relaxation (fluffing of plumage, shortening of the neck, general diminution of activity, intermittent closure of eyes) and

Table 1

	N	Staring down	Pecking	Yawning	Squatting	Relaxing	Sleeping
Loci eliciting preening (%)	37	27	16	49	43	54	8
Loci not eliciting preening (%)	165	5	4	4	7	10	0
Fisher's or χ^2 one d.f., P	$< 0{\cdot}001$	$\approx 0{\cdot}001$	$< 0{\cdot}001$	$< 0{\cdot}001$	$< 0{\cdot}001$	$< 0{\cdot}01$	

occasional sleep. We find that several, and sometimes all, these component patterns can often be elicited from single loci with the same stimulation strength, usually less than 50 μamp, either as a result of a single stimulation train or more frequently in the course of several consecutive trains. In Table 1 all 202 loci so far explored have been classified into those which gave preening and those which did not. Within each class of loci the percentage which yielded the different other components is shown. All the component patterns were associated with electrodes eliciting preening rather than with those which did not, and the association is significant. A similar relationship may also hold for mandibulation, shaking the body and head, wagging the tail and shaking the foot, but because these patterns are also frequent during control periods without stimulation, a decision is difficult. No such association could be detected for some twenty-five other various behaviour patterns examined.

It is significant that the preening positive points clustered in several discrete anatomical areas of the telencephalon and diencephalon and that ten electrodes responsible for more than half the entries in the non-preening class also lay within or close to these areas. There is not sufficient information to decide whether the associations of components are stronger in some areas than in others, although some evidence points in this direction.

The conclusion that these diverse behaviour patterns reflect the activation of a more or less unitary system leading to de-arousal, and are not a result of the simultaneous stimulation of contiguous but otherwise unrelated neural systems, is supported by observations on unstimulated normal gulls which suggest a high temporal and sequential association between the component patterns including sleep. Furthermore, preliminary experiments indicate that at least two hypnotic drugs, pentobarbital sodium and tribromoethanol, given systemically, reliably elicit the syndrome just described. Preening, staring down and pecking the ground are also the patterns most often involved in displacement behaviour in gulls[13,14]. A similar relationship seems to hold in some other species.

In the cat Parmeggiani[15] stimulated several different and separate areas of the forebrain and brainstem and obtained a behavioural complex consisting of sniffing, grooming, yawning, lying down, curling up, dozing and sleeping. He emphasizes that this behaviour is normal in unstimulated cats. Rowland and Gluck[16] present some evidence that in a certain conditioning procedure grooming replaced the synchronization of the electroencephalogram shown by sleeping cats when these were tested awake. Again, Leyhausen[17] lists grooming, sniffing and lying down as displacement behaviour for the cat.

For the rat, Caspers[18] has shown that grooming and some other unfortunately unspecified "motorautomatisms" are associated with shifts in the cortical d.c. potential making the surface positive, which otherwise are typical of sleep, while shifts towards a negative surface are characteristic of the waking animal. Grant[19] mentions grooming, digging and sniffing as typical displacement activities of rats.

These facts suggest that grooming or preening and certain other movements are largely controlled by neurophysiological mechanisms which are also responsible for de-arousal and sleep. On the other hand they are often involved in displacement behaviour. There is little doubt, however, that the behavioural situations leading to displacement, that is, conflict, frustration and thwarting, are effective in increasing arousal[20,21]. I suggest that the occurrence of at least some displacement activities is the reflexion of a homeostatic process operating towards cancelling the arousal increment so generated, through the activation of an arousal inhibiting system. The existence of arousal homeostasis has been suggested by Berlyne[22], who also marshals supporting empirical evidence. Such regulation appears logically necessary if arousal is correlated with the rate at which information is handled and if the nervous system is considered as a communication channel of restricted and specific capacity where for maximum efficiency the information handling rate must be held within certain limits[23,24].

The striking occurrence of sleep as displacement in several species[5] may be regarded in this context as a regulatory overshoot. Why grooming and other patterns should be activated by a neural de-arousal system is functionally not obvious, but perhaps these types of activities are conducive to de-arousal in a similar way to other activities[25-27], possibly through stimulus reduction (cut-off[28]), switch of attention to stimuli of little novelty[22] or generation of repetitive stimulation[29,30].

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