Abnormal patterns of displacement activities: A review and reinterpretation

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ABSTRACT
A series of important theoretical contributions flourished in the years 1950–1970 about displacement activities—those 'out-of-context' actions expressed by organisms in stressful situations. Nothing really new has appeared thereafter. Although the models address different issues, such as causal factors of displacement, it appears obvious that they do not provide a unified (coherent) approach; they often explain the same phenomena using very different means and turn out to be contradictory on several points. In addition, some problems currently remain unsolved, especially concerning the fact that displacement activities exhibit 'abnormalities' of expression in comparison with the same activities performed in usual context. Each model is here described and criticized in order to evaluate its explanatory power and allow the identification of specific limits. A new, integrative model – the Anticipatory Dynamics Model (or ADM) – then attempts to overcome the failures of previous models. The ADM suggests that abnormal patterns of displacement activities result from attentional interference caused by a thwarting experience or conflicting motivations. At least one theoretical prediction of the ADM can be differentiated from that of any other model.

1. Introduction

Displacement activities are banal behaviours in the repertoire of a species that individuals perform when they are thwarted in achieving a goal – e.g. the expected food is absent – or when they are subject to simultaneous influence of antagonistic motivations, e.g. the attack-flight conflict facing a rival. These behaviours are traditionally considered 'out-of-context' because they prove unrelated to the ongoing activity. For example, sleeping acts during a flight in avocets (Recurvirostra avosetta), ventilating acts of an empty nest in male sticklebacks (Gasterosteus aculeatus) when sexually thwarted, etc. (Tinbergen, 1951). In a majority of articles devoted to displacement activities, different causal explanations of these activities have been put forward (e.g. Tinbergen, 1951; Van Iersel and Bol, 1958; Rowell, 1961; Sevenster, 1961; McFarland, 1966b; Schino et al., 1996).

In this paper, I am interested in explaining the cause of this evidence that displacement activities often exhibit 'abnormal' patterns in comparison with the same activities carried out in usual context. The term 'abnormal' does not refer to any behavioural pathology but merely means that displacement activities are reported as more intense (sometimes 'frantic'), incomplete (rough or non-finalised) and of shorter duration. For instance, a cock might stop fighting another cock and start vigorously pecking at grains on the ground without swallowing them (Tinbergen, 1951). In the same vein, a fowl prevented from accessing its expected food might 'frantically' start preening its feathers, each preen being of shorter duration than in 'non-frustrated' animals (Duncan and Wood-Grush, 1972a).

What is the cause of abnormal patterns of displacement activities? Although most theories date back to several decades, this question is still a topical one, and there are as many answers as models. While a majority of models accounts for the appearance of such abnormal patterns, others do not. Indeed, some cases have been reported where displacement activities seemed to exhibit 'normal' features (e.g. Leyhausen, 1973; Rowell, 1961). For instance, the frequency of displacement preening in chaffinches (Fringilla coelebs) seems to be, as expected, positively correlated with the quantity of water received on their feathers in a conflict situation (Rowell, 1961). Tinbergen’s (1951) overflow model, which predicts the appearance of abnormal patterns, was then progressively replaced in the literature by Andrew’s (1956) disinhibition model, which suggests that such abnormal patterns do not exist. This debate was maybe exaggerated due to minimization of abnormalities by disinhibitionists (Duncan and Wood-Grush, 1972b; Roper and Posadas-Andrews, 1981). But to date, there is not yet satisfactory explanation of such abnormalities.

It is here hypothesized that abnormal patterns of displacement activities result from attentional interference induced by the thwarted motivation or the conflicting motivations on the...
displacement unfolding. The hypothesis is original and stems from a model, the Anticipatory Dynamics Model (ADM), I have previously developed to account for behaviour of organisms subject to simultaneous influence of several motivations (Anselme, 2007). Basically, the ADM states that an individual’s motivational interactions are due to the limitation of the individual’s attentional resources and that anticipation determines how these resources are shared. The ADM is here used to suggest a plausible answer to five unresolved issues about abnormal patterns of displacement activities as well as to provide a new, integrative approach to displacement. It is advanced that the explanatory power of traditional models remains weak because they ignore important variables for the understanding of behaviour. The ADM currently remains hypothetical but allows formulating an original prediction to contrast it with all other models concerning the cause of abnormal patterns of displacement activities. After describing and criticizing traditional models, I define five unresolved issues and attempt to provide them a plausible answer using the ADM.

2. Traditional models: a review

2.1. The overflow model

Tinbergen (1951, 1952) saw motivation as a non-specific ‘energy’ because different behavioural pathways can exploit it. When this ‘energy’ is in surplus in a non-releasable pathway (due to thwarting experience or conflicting actions), he said, it discharges in another (and releasable) pathway. The resulting ‘irrelevant’ action was then considered as a displacement. In this view, the displacement activity is always assumed to occur because of a surplus of motivational ‘energy.’ Tinbergen (1951, p. 114) indeed reported that all known cases of displacement indicate a surplus of motivation. Abnormal patterns are interpreted as an unavoidable consequence of the animal’s excitation.

Unfortunately, some findings show that displacement activities can also occur when the motivations involved are of low intensity, that is, when these motivations are not in surplus. For instance, Van Iersel and Bol (1958) studied displacement preening in terns (Stern). They frightened incubating terns using an alarm cue and suggested that the landing distance of the birds from the nest depended on the intensity of their incubating motivation. The observations indicate the occurrence of displacement preening in strongly frightened terns landing close to the nest (whose incubating motivation is of high intensity) as well as in weakly frightened terns landing far from the nest (whose incubating motivation is of lower intensity). Of course, it might be argued that considering the landing distance as a reliable indicator of the birds’ incubating motivation and fear looks like a postulate. But the use of behavioural indicators of psychological processes is the only way to learn about the studied phenomena (and that procedure is also applied to the studies reported thereafter). Another example comes from a study by Duncan and Wood-Grush (1972b), which showed that the type of displacement in fowls differed according to the intensity of their feeding motivation during thwarting. When the fowls were highly motivated to feed (24h-deprivation period and 10-day training to obtain food), they mainly exhibited displacement pacing when prevented from accessing to food the day after. In contrast, when the fowls were less motivated to feed (6h-deprivation period and only 3-day training to obtain food), they mainly performed displacement preening when thwarted. The hypothesis that a surplus of motivation might have been already reached after 6h deprivation is implausible. This would oddly mean that hungri ness of fowls does not change between 6 and 24h deprivation. If this were true, why would they exhibit their ‘frustration’ differently in both conditions? Interestingly, displacement preening observed after a 6h-deprivation period has been shown abnormally intense (Duncan, 1970; Duncan and Wood-Grush, 1972b).

2.2. The disinhibition model

Some difficulties related to the overflow concept have led ethologists to suggest an alternative theory of displacement activities, where disinhibition plays a central role (e.g. Andrew, 1956; Van Iersel and Bol, 1958; Sevenster, 1961; Rowell, 1961; Zeigler, 1964). In its general version, the disinhibition model is straightforward: when two motivations are in equilibrium, they inhibit one another, and a third-priority motivation is disinhibited as a consequence. The activity resulting from the disinhibition process is the displacement. In contrast with the overflow model, it is here assumed that displacement activities possess own causal factors; that they are normal activities whose opportunity of expressing has arrived. As with the activities performed in usual context, the environment has indeed been shown to determine the choice and intensity of displacement activities. For instance, Räber (1948) observed that, during a fight, domestic turkeys (Meleagris gallopavo) exhibit displacement feeding when food is available and displacement drinking when water is present (for other examples, see Hinde, 1952; Morris, 1954; Andrew, 1956; McFarland, 1965). Wet feathers in chaffinches (F. coelebs) increases the frequency of displacement grooming (Rowell, 1961) and elevation of the carbonic gas concentration in water intensifies fanning of eggs in male sticklebacks G. aculeatus (Sevenster, 1961).

Without denying the causal role of the environment in displacement activities, it is not sure whether they can be considered ‘normal.’ Of course, it is possible to modify the expression of a displacement activity by modulating its own causal factors, as shown above (e.g. Rowell, 1961; Sevenster, 1961). However, the disinhibition model cannot explain why the intensity of conflicting motivations or that of the thwarted motivation also affects the displacement activity. For instance, the frequency of gakel-calls increases with magnitude of food deprivation in thwarted fowls (Zimmerman et al., 2000a,b). The same remark is also worth making when the thwarting experience turns on dust-bathing behaviour (Schenk et al., 1983). The influence of thwarted/conflicting motivations is even sometimes concretely observable. For instance, the dorsal spines of a male stickleback that performs displacement digging during a fight remain erected, a sign of aggressiveness, while they are not when digging arises in usual context, e.g. to search for food (Tinbergen, 1951).

Finally, the idea that the displacement activity necessarily corresponds to the animal’s third motivational priority has been challenged. Wilz (1970) observed that the first and third most frequent actions prior to courtship in male sticklebacks were respectively pushing and bringing material for nest construction. Their most frequent actions during courtship were fanning, gluing, and creeping through. Although the action of pushing was sometimes observed during courtship, ‘the third most frequent activity prior to courtship, bringing, was never recorded during a courtship sequence’ (Wilz, 1970). Furthermore, observations in several species of monkeys show that the most frequent displacement activities that occur during or immediately after a fight are scratching and self-grooming (Poirier, 1974; Aureli et al., 1989; Aureli and van Schaik, 1991). This might let to think that monkeys carry out their third motivational priority at that time since body care activities are the common thing to do after an aggression. Yet, this explanation should be dismissed insofar as reconciliation and redirection reduce the rate of such activities (Aureli and van Schaik, 1991; Maestripieri et al., 1992; for a review, see Aureli et al., 2002).
2.3. The attentional disinhibition model

According to McFarland (1966a,b, 1985), an animal subject to the influence of conflicting motivations or thwarted somehow experiences ‘frustration’ and thus switches its attention on other stimuli. Displacement would then be the activity disinhibited by the attentional switch. The mechanism of attentional disinhibition is rather complex. In a few words, it is supposed that animals learned mental representations – called output copies – of the consequences of their behaviours in such a way that animals are able to expect those consequences in an adequate environment. The output copies are thereby always correct in such an environment; the feedback discrepancy between the output copy and the real consequences equals zero. Now, if the environment is not so responding, as with thwarting or conflicting situations (where what is obtained is not what was expected), the feedback discrepancy is no longer equal to zero, and this induces a switch of attention on peripheral cues. Animals therefore carry out a displacement activity in relation to these peripheral cues. However, as the displacement activity is ‘out-of-context’, its appropriate consequences are not observed by animals, which are subject to a new attentional diversion towards the initial context. McFarland (1986b) argues that this quick switch process explains why displacement activities are often reported as to be incomplete and of short duration.

Other authors made the assumption that an attentional switch explains activity transitions. For instance, Culshaw and Broom (1980) suggested that distractibility in chicks decreases after a few seconds of a bout of behaviour (attentional ‘locking’) and increases at the end of the bout (attentional ‘unlocking’) in order that animals can attend to a greater variety of inputs. Their results (discussed in Section 5.3) are highly relevant for the model (ADM) developed in this paper, but the interpretation should be taken cautiously. There is no clear evidence that activity transitions depend on such an all-or-nothing process. When an activity takes over another, the observed transition is usually gradual rather than abrupt, contrary to what a switch process would suggest. That is, the time and intensity of the transition are a function of the second activity’s readiness (Roper and Crossland, 1982). Hogan (1989) argues that empirical findings supporting the time-sharing hypothesis – or the existence of abrupt, spontaneous changes of activity – derive from ambiguous methodologies and may systematically be interpreted otherwise (see also Crawford and Colgan, 1989). To make the attentional switch hypothesis plausible, it should be shown, for instance, that distractibility in chicks does not vary within a bout of behaviour, but several results do not confirm this idea (Van Iersel and Bol, 1958; Van Rhijn, 1977).

McFarland’s idea that attention and anticipation are causal factors of displacement activities is original. It is also at the heart of the model (ADM) proposed further. However, besides the model’s intrinsic complexity that makes it difficult to test, some doubts should be expressed about its ability to account for the great intensity often reported about displacement activities. Let us remember that a positive feedback discrepancy is the sole condition for a displacement activity to occur. Logically then, the greater this feedback, the more intense should be the resulting displacement. Unfortunately, the feedback is only sensitive to the absence of matching between an animal’s output copies and the consequences of its behaviour, not to the motivations involved. In the literature, the intensity of displacement is never mentioned as depending on environmental inadequacy.

2.4. The post-inhibitory rebound model

It is usually admitted that ‘all behavioural transitions comprise inhibition of one activity and disinhibition of another’ (Kennedy, 1985). When an activity ceases, the post-inhibitory rebound of another is therefore expected to occur. Interestingly, the post-inhibitory rebound of a previously inhibited motivation can reach a higher intensity than that it had before being inhibited. Kennedy (1985) therefore suggests that such a rebound would explain the origin of displacement activities as well as the occurrence of abnormal patterns. Indeed, the post-inhibitory rebound of a motivation might be suddenly induced by the inhibition of conflicting motivations.

However, Roper (1985) finds this scenario rather strange: if a post-inhibitory rebound necessarily followed all activity transitions, why would its consequences be only observed with displacement activities? It should be expected for each transition of activity at any time. A rat may stop drinking to commit into another activity, such as grooming or exploring. Yet, abandoning the former behaviour does not lead to any abnormality in performing the latter (see also Roper and Crossland, 1982; Roper, 1984), contrary to what would be expected if the transition was due to an abrupt disinhibition (see previous comments, Section 2.3). Maybe on account of that, Kennedy’s view has hardly got a response in the literature.

2.5. The anxiety model

After Schino et al. (1996), displacement activities are the expression of ‘anxiety’. They found that an anxiolytic treatment with lorazepam reduces the rate of displacement activities in social situations in male macaques (Macaca fascicularis). In contrast, the use of FG 7142, known for its anxiogenic effects in humans, increases the frequency of displacement activities. There is here no reference to abnormal patterns. But it might be suggested that they also result from ‘anxiety’. It is reasonable to think that anxious animals produce, like humans, inappropriate and bizarre actions due to uncertainty about the correct way of doing things. As they point out, ‘uncertainty and anticipation of unpleasant events are crucial factors in the causation of displacement activities’ (Schino et al., 1996).

The main problem with this view is that no motivational mechanism is provided. The psychological significance of ‘anxiety’ is not to be neglected, as that of ‘frustration’ often mentioned in the study of displacement activities. But how ‘anxiety’ (and also ‘frustration’) is related to the occurrence of displacement activities currently remains unclear.

2.6. The dopamine model

It now seems to be established that dopamine releases can occur when an individual anticipates the arrival of pleasant as well as of unpleasant events (e.g. Berridge and Robinson, 1998; Di Chiara, 2002; Rada et al., 1998; Schultz, 1998). There is evidence that this process is a crucial factor in the causation of displacement activities. When rats are placed in a schedule of food delivery, an increase in endorphins and plasma corticosterone is observed compared with rats given non-scheduled food (Le Moal and Simon, 1991). However, a decrease in these hormones appears in individuals performing displacement activities in such a situation (e.g. Brett and Levine, 1979; Danzter and Mormede, 1981; Wallace et al., 1983; Tazi et al., 1988). It is known that dopaminergic terminal lesions in the nucleus accumbens, a region of the ventral striatum in the brain, suppress the increase in corticosterone of rats subject to a schedule of food delivery (Wallace et al., 1983). This might therefore indicate that dopamine is required for displacement activities as well as for their associated hormonal responses (Le Moal and Simon, 1991). Indeed, dopamine neurons present specific receptors to corticosterone allowing them to be informed, and also more receptive, to stressful situations (e.g. McEwen et al., 1986; Brinton...
The fact that dopamine plays a role in the exhibition of displacement activities allows considering anticipation of unpleasant events as their causal factor, a view akin to Schino et al.'s (1996). When dealing with a situation is too difficult, organisms therefore prefer to commit into another activity.

Currently, there is an agreement that displacement activities have a de-arousing function, a way of decreasing plasma corticosterone levels and of blocking the pain-inhibitory systems (e.g. Brett and Levine, 1979; Dantzer et al., 1984; Tazi et al., 1988). This allows the individual to deal with stressful situations. Displacement activities are therefore adaptive because an inappropriate action may be dangerous and is always ineffective. According to Le Moal and Simon (1991), stress-reducing properties of displacement activities are caused by the enhanced activation of dopamine neurons. Panksepp (1998) puts forward the same idea: the cause of displacement activities would be over-arousal of the brain's SEEKING system, which mainly includes dopamine's neural network. Lesions of the lateral hypothalamus as well as chemical blockade of dopamine receptors indeed reduce the appearance of such behaviours (Wayner et al., 1991).

This evidence that dopamine is connected with displacement does not indicate that the old models turn out to be not necessary any more. Approaching a direct, physiological level of analysis of behaviour is certainly useful to correlate an individual's actions with its biological and evolutionary constraints. But those correlates will never explain why the individual does what it does at a particular place and time in the environment. The study of biological and evolutionary constraints is essential in that displacement is not just the side-effect of perceptual or cognitive constraints. However, there are necessarily psychological reasons (stress, aversion, etc.) why organisms adopt particular behaviours in specific circumstances.

### 3. The myth of equilibrium

Before taking stock of theories related above and going further, I want to demystify a widespread idea. The most influential theories – i.e. the first three described – explicitly state that displacement activities arise on condition that the conflicting motivations are in equilibrium of intensity. Tinbergen (1951, p. 116) describes the hesitating behaviour of a male stickleback (*G. aculeatus*) facing a dummy in these terms: just before attacking the dummy again, 'the male performs displacement digging. This shows, therefore, that displacement digging occurs when the two drives involved [fight and flight] are in exact equilibrium.' It is sometimes argued that drives of equal strength lead the animal's behaviour to become ambivalent or even blocked, making possible the appearance of another behaviour (the displacement activity) controlled by a different motor command (McFarland, 1966b).

In reality, the idea that equilibrium of intensity is required for the causation of displacement activities resembles more a postulate than scientific evidence (Rowell, 1961). Rowell admits this postulate while pointing out that reliable data are difficult to obtain. Recognizing a conflict situation is not even easy without taking inter-individual differences into account among the studied animals (Hinde, 1970, Chapter 16). A study by Kruijt (1964) about fighting cocks (*Gallus gallus*) really calls the postulate of equilibrium into question. Kruijt observed a positive correlation between some of the displacements produced during a cockfight and the final outcome (winner or loser) for each cock (Fig. 1). Winning cocks preferentially expressed their displacement by feeding during the fight, while losing cocks did more displacement preening. This result is essential to our purpose: if winners and losers statistically favoured such-and-such a displacement activity during the cockfight, this means that each cock perceived itself – even unconsciously – as a subsequent winner or loser before their fight terminates. The attack-flight antagonism was then differently represented in 'optimist' and 'pessimist' cocks. Optimist cocks perceived themselves as dominant, their tendency to attack was stronger than that to flee. Conversely, pessimist cocks perceived themselves as subject to their adversary, their tendency to attack was weaker than that to flee. This is to say that interference can occur with motivations of unequal intensities, as noticed by Hinde (1970, Chapter 17). Such a result is opposed to the general agreement that displacement activities necessarily arise in equilibrium.

I do not deny that displacement activities may occur in equilibrium; I just challenge the idea that they require equilibrium to arise. For instance, displacement nest digging in male stickleback (*G. aculeatus*) was found to happen most frequently at the boundaries between two territories, where the tendencies of rivals to attack and flee are supposed to be of equal intensity (Tinbergen and Van Iersel, 1947; reported by Zeigler, 1964). This observation indicates that displacement activities also sometimes occur at other places, where both tendencies should be not equivalent to each other.

### 4. Unresolved issues

Each model described above predicts certain properties of displacement activities – e.g. the disinhibition model takes environmental influences into account, etc. – but fails to correctly predict others, e.g. the disinhibition model denies the existence of abnormal patterns. I do not intend to repeat what I have already said in the previous sections, but, rather, to summarise the problems currently remaining unresolved which would justify the elaboration of an integrative model of displacement activities. In my opinion, besides the origin of displacement itself, the five unresolved problems are as follows:

- Why do abnormal patterns appear with motivations of high intensity as well as with motivations of lower intensity?
- Why is the occurrence of abnormal patterns related to motivational conflict or thwarting?
- Why does the displacement activity not necessarily correspond to an individual's third motivational priority?
- Why does a displacement activity only rarely appear without abnormal patterns?
- Why does the displacement activity not necessarily occur in motivational equilibrium?
In next section, a new model of displacement activities is presented. I will then come back to these unresolved issues to attempt to answer them using that model.

5. Another view: the anticipatory dynamics model

In the literature, several models are compatible with the observation of abnormalities in the execution of displacement activities, that is, their high speed and incompleteness. Despite the number of processes described, all these models consider that such abnormalities depend on a unique variable: motivational intensity. Abnormalities would result from a loss of motor control induced by the animal’s general excitation, usually referred to as ‘frustration’ or ‘anxiety.’ However, the five unresolved issues mentioned above indicate that this simple, intuitive idea does not allow scientists to circumscribe all observations. In order to bring an answer to these issues, a new model, the Anticipatory Dynamics Model, developed elsewhere in another aim (Anselme, 2007), is now considered. Its main difference with traditional models of displacement activities is to suggest that the explanation of abnormal patterns involves considering their exhibition as a result of a combination of several variables. The ADM constitutes a coherent articulation of phenomena which play a central role in behaviour: anticipation, attention, motivation, causal factors of motivation, and reactivity. All these phenomena are known but often undifferentiated within models that consequently do not really explain how behaviour can emerge from their interconnections. This lack of theoretical nuances of traditional models is thus viewed as the cause of the encountered explanatory problems. Let us begin by briefly presenting the ADM.

5.1. The concept of A-threshold

It is admitted that for any behaviour to occur, its motivation must reach a given intensity, called reactivity threshold (or R-threshold), whose value may vary according to learning or context (e.g. Balleine, 1992; Hogan and Van Boxel, 1993). For example, rats need to learn the incentive value of food by experiencing it before seeing that reward as an attractive consequence of a particular action (Balleine, 1992). Once these animals have had their first contact with the food, its attractiveness then remains the same, irrespective of the motivational intensity of the rats. This indicates that the reinforcing value of food seems to affect the reactivity threshold of the feeding motivation rather than that motivation in itself. However, according to the ADM, another type of threshold also needs to be taken into account to explain an organism’s behaviour when several of its motivations are simultaneously activated: the anticipatory attention threshold (or A-threshold). The concept of anticipatory attention merely means that, in some cases, an animal’s attention may be focused on stimuli of great interest because of the intensity with which some information is anticipated about them.

Before describing the model, the neuropsychopharmacological evidence in favour of that concept needs to be briefly stated. It appears that the neurons involved in attentional performance, such as cholinergic neurons of the basal forebrain (e.g. Himmelheber et al., 2001; Sarter and Bruno, 1999; Turchi and Sarter, 1996), are stimulated by mesolimbic dopamine, whose correlation with anticipation is now well established (e.g. Berridge and Robinson, 1998; Franken et al., 2005; Ranaldi et al., 1999; Sarter and Bruno, 1999). Indeed, an increase in dopamine levels of the ventral tegmental area, a midbrain region, has been essentially observed in animals before presentation of sucrose (Kosobud et al., 1994), food (Phillips et al., 1991), cocaine (Gratton and Wise, 1994), and heroin (Kiyatkin et al., 1993) in comparison with the consummatory phase of behaviour. Stress and punishment-associated stimuli (such as a light and tone) are also known to increase dopamine levels in the nucleus accumbens, a brain region receiving neuronal projections from the ventral tegmental area (Di Chiara, 2002). The involvement of dopamine in anticipation of positive and negative events is now a widespread idea (e.g. Di Chiara, 2002;Rolls, 1999). On the other hand, dopamine’s role is larger than that and notably seems to bring about an indirect activation of cholinergic neurons of the basal forebrain. These neurons produce acetylcholine when animals are subject to attentional tasks (Sarter et al., 1999) and their excitability is improved in the presence of dopamine (Sarter and Bruno, 1999).

In fact, cholinergic discharges might be independent of the attentional demands of a task in itself (Passetti et al., 2000) but related to what organisms are able to anticipate at a time. Himmelheber et al. (2001) thereby recorded substantial fronto-parietal releases of acetylcholine when rats were transferred into an operant cage, where a reward can be obtained, whatever the task difficulty and even the repetitions of the procedure. On account of its psychological significance, the ‘dopamine–acetylcholine axis’ is therefore a plausible neuropharmacological correlate of anticipatory attention.

In the ADM, dopamine levels in the nucleus accumbens represent the intensity of causal factors of motivation, not motivation in itself. The intensity of dopamine required to stimulate cholinergic neurons of the basal forebrain is the A-threshold. When dopamine levels overcome the A-threshold’s value, a motivation is induced, that is, the psychological process allowing an individual to become more receptive to (or to ‘want’) particular stimuli. Motivational intensity is all the higher because the A-threshold’s value has been overcome (Fig. 2). This is to say that the A-threshold designates the intensity of a motivation’s causal factors from which these causal factors become converted into motivation. Causal factors under their A-threshold remain non-motivating as well as unable to affect behaviour. Contrary to what is traditionally suggested, there is here no a priori equivalence between motivation and its causal factors; the level zero of a motivation is not necessarily the level zero of its causal factors. The next section describes the conditions in which such non-equivalence can be expected to occur.

5.2. Dynamical properties of A- and R-thresholds

If all causal factors were inactivated at a time, the ADM would imply that the A-threshold of all motivations is equal to a minimum value, close to zero. This scenario does not probably make sense, but to keep it in mind may be useful to understand how the ADM works. On this basis, the ADM predicts that when a motivation is the sole to be activated, because of an increase in its causal factors, this motivation and its causal factors are of equal intensity (Fig. 3A).

As said, the A-threshold’s value of these causal factors (CF1) is supposed to be close to zero. But the newly induced motivation M1
raises the A-threshold of concurrent causal factors (CF2), even if they are absent at that time, because of the limitation of attentional resources in organisms (see below). To say that an increasing motivation raises the A-threshold of causal factors of other motivations concretely means that it makes the appearance of concurrent motivations in raising the A-threshold of their causal factors harder. Indeed, concurrent causal factors have to reach a higher intensity to be converted into motivation than when any other motivation is not activated. From a neuropsychopharmacological viewpoint, this would mean that when the object of one motivation activates the dopamine–acetylcholine axis, the available resources on this axis are reduced for the object of another motivation.

The ADM predicts that when two or more motivations are simultaneously activated, these motivations and their causal factors become of unequal intensity (Fig. 3B). If the causal factors CF2 of a motivation M2 are able to overcome their A-threshold, previously raised by M1, then M2 becomes, in turn, capable of raising the A-threshold of causal factors CF1. Owing to their simultaneous activation, M1 and M2 are thereby of smaller intensity than that prescribed by their corresponding causal factors. According to the ADM, mutual inhibition of motivations is supposed to be due to limited attentional resources in organisms. Reducing attractiveness of a stimulus might be the price to pay when the organism also becomes interested in another stimulus. Some empirical findings seem to support such a view. Cosgrove et al. (2002) report that cocaine self-administration in rats is significantly reduced when these animals are also allowed to perform wheel-running in their cage. Such a phenomenon is observed even though the available period of time is sufficient to allow the rats to self-administer cocaine at the same rate as before. Conversely, the rats spend less time in the wheel when they have the opportunity to self-administer cocaine. The ADM explains mutual inhibition because simultaneous activation of two or more motivations raises their A-threshold at a higher intensity than zero.

As pointed out above, the dynamics of A-thresholds depends on attentional capabilities, which are a limited resource in organisms. This attentional limitation of organisms means that they can hardly allocate resources to more than one thing at a time. The limitation of attention has been highlighted in humans (e.g., Hirst and Kalmar, 1987; Noble et al., 1981; Shallice et al., 1985) as well as in animals (e.g., Dukas and Kamil, 2001; Lejeune et al., 1999; Maki and Leith, 1973; Zentall et al., 1997). Such a constraint has an immediate, automatic repercussion on the organism’s motivations. When a motivation increases, because the anticipatory attention process boosts it, this causes the inhibition of the organism’s other motivations due to a raise of their A-threshold. Conversely, when a motivation decreases because its object becomes of weaker interest, there is a disinhibition of the organism’s other motivations due to a lowering of their A-threshold. Of course, if we admit that displacement activities result from motivational interactions, inhibition and disinhibition are likely to be partial rather than total most of the time. The dynamics of A-thresholds must be therefore carried out at moderate raising and lowering rates. High rates would suppress the possibility for motivations to interact (what leads to an unrealistic description of reality), and low rates would make motivational interactions permanent (what is also unrealistic). In all likelihood, the most plausible scenario is an in-between. Nothing more will be said here on this point but a mathematical formalism of the model is to be found in Anselme (2007).

The expression of behaviour implies that its motivation reaches a critical intensity termed R-threshold. This variable seems to depend on causal factors unrelated to those of motivation and they will not be considered here (see Balleine, 1992; Pelchat et al., 1983). However, when multiple motivations are involved, the dynamics of R-thresholds is predicted to depend on that of A-thresholds. As represented above in Fig. 3, both A- and R-thresholds are associated with the causal factors of any motivation in such a way that the A-threshold always designates a smaller intensity of the causal factors than the R-threshold. It is a logical postulate: the A-threshold needs to be of smaller intensity than the R-threshold to allow organisms to ‘want’ to act as well as to pay attention to the object of their action before carrying it out. Given this postulate and the mechanism of inhibition/disinhibition described above, anticipatory dynamics has an inevitable consequence: when a motivation’s causal factors overcome their A-threshold, this raises the R-threshold of concurrent causal factors. Indeed, the R-threshold of concurrent causal factors is in a way ‘pushed’ by the raising A-threshold. The raise of a motivation’s R-threshold may explain why people’s reaction times are slowed down when they do two simultaneous tasks (see Baddeley, 1990).

5.3. Illustration through an example

Before coming back to displacement activities, it is useful to illustrate the explanatory power of the ADM through a concrete study, which is related to the problem of abnormal patterns of activity in some respects. Culshaw and Broom (1980) studied the responsiveness of 6-day-old chicks to sudden illumination of a 3 W torch-bulb during feeding and preening. Illumination of the bulb indeed brings about a startle response that inhibits the ongoing activity for a time. In one group, bulb illumination occurred 2 s after the chicks had started feeding or preening, and in the other group, it happened when the end of the feeding or preening bout was imminent—the mean bout-duration of those activities was previously assessed in undisturbed chicks.

With respect to feeding, Culshaw and Broom (1980) observed that the chicks disturbed at the end of the bout remained longer immobile fixing the illuminated bulb than the chicks disturbed at the beginning. The ADM easily explains the difference of feeding inhibition reported here. The feeding motivation at the start of the bout is high and therefore strongly raises the A-threshold of any concurrent motivation’s causal factors. Thus, illumination-induced
causal factors remain insufficient to be converted into an intense, stable motivation. The attentional focusing of chicks on the bulb is then limited. On the contrary, the chicks disturbed at the end of the bout exhibit a reduced feeding motivation, which has significantly lowered the A-threshold of concurrent causal factors. The resulting effect of bulb illumination is then greater.

In the case of preening, the chicks disturbed at the end of the bout ceased their activity almost immediately while those disturbed at the beginning continued to preen for some time but at a higher frequency after bulb illumination. Here also, the inhibition of preening is easier at the end of the bout than at the beginning. Interestingly, the chicks that exhibited a startle response at the beginning of the bout seemed to perform an abnormal pattern of preening similar to that observed during displacement preening. The ADM predicts that the origin of such an abnormal pattern is identical in both cases: although preening is too strongly motivated to be totally inhibited, its unfolding is impeded by an attentional focus of chicks on another stimulus (here, bulb illumination). As a result, preening is performed with obvious signs of nervousness.

6. Main differences with the attentional disinhibition model

Does the ADM amount to McFarland’s (1966b) attentional disinhibition model? It was shown above that McFarland’s model suggests that an individual subject to motivational conflict becomes frustrated and starts paying attention to peripheral stimuli, causing disinhibition of a displacement activity’s motivation. As the expected consequences of the individual’s actions do not occur, this action is quickly given up. This model differs from the ADM on many points but two of them prove to be essential.

To begin with, there are reasons to think that McFarland’s model is perceptual rather than attentional. The logic behind the model remains identical if we say that an individual subject to motivational conflict becomes frustrated, looks elsewhere for a while, and then returns to conflict when the individual sees that the expected consequences of its action have not occurred. Of course, perceiving any situation requires for an individual to allocate some attentional resources to it. But attention is not here the explanatory factor: McFarland is in no way interested in the properties of attention, especially the property of divided attention. Yet, attentional resources are limited and this needs to be taken into account in any attentional model devoted to motivational conflicts. McFarland notices that ‘the more an animal attends to certain aspects of the environment the less it attends to other’ as a prerequisite to ‘frustration’-dependent attentional switch, but the process is presented as a physical rather than cognitive constraint.

The ADM is in accord with McFarland’s idea that attentional diversion disinhibits the displacement activity’s motivation and leads to the inhibition of conflicting motivations. But our model does not agree with the mechanism of disinhibition subsequently defined by McFarland (1969, 1985). This mechanism is indeed somewhat unusual (see Ludlow, 1976; Houston, 1982; Roper and Crossland, 1982) and incompatible with the principle of divided attention. Fig. 4A illustrates McFarland’s disinhibition process and Fig. 4B its usual representation, which is also that working in the ADM. According to the ADM, when a motivation M2 increases in intensity, it raises the A-threshold of a motivation M1. This increase corresponds to the inhibition of M1, as noticed in Fig. 4B. In attentional terms, this means that attention allocated to the object of M2 can no longer be provided to that of M1. In contrast, McFarland thinks that when M2 increases in intensity, it is content with ‘camouflaging’ the influence M1 previously had on behaviour, without affecting M1 in any way. M1 is therefore not really inhibited. If we suppose that M2 is disinhibited by attentional diversion, how is it possible that less attention about the object of M1 does not reduce M1? In conclusion, McFarland’s model of attentional disinhibition does not integrate the principle of divided attention, contrary to the ADM.

A second difference with the ADM is the inability of McFarland’s model to account for abnormal patterns of displacement activities, in particular their unusual intensity. As already said, the discrepancy between an animal’s mental representations and the real world can explain why displacement occurs or stops, but not why it is performed with greater intensity than the same activity in usual context. McFarland suggests that recognition of such a discrepancy by the animal allows displacement to be of short duration. But a distinction must be here established between the duration of an activity conceived as a displacement and that of its possible sub-activities. It is one thing, for a fowl, to take less time to perform an uninterrupted sequence of feathers preening acts, it is quite another to reduce each preening act within such a sequence. McFarland could explain the former aspect (time reduction of the sequence), not the latter (time reduction of each act in the sequence), which has been observed yet (Duncan and Wood-Grush, 1972a).

7. The attentional interference hypothesis

With respect to the origin of displacement activities, the ADM is compatible with the idea of attentional diversion, which probably results from ‘anxiety’. However, the ADM provides an original hypothesis with respect to the origin of abnormal patterns of displacement activities: they would result from attentional interference caused by the thwarting experience or conflicting motivations (Fig. 5A and B).

When the object of an animal’s motivation is determining its ongoing behaviour, the animal is assumed to be preoccupied by this object, which may be some food, a sexual partner, etc. It is here merely argued that if this behaviour is suddenly prevented somehow, its object will continue to affect the animal’s subse-

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**Fig. 4.** (A) The process of disinhibition according to McFarland (1969, 1985): motivation M2 dramatically increases and ‘camouflages’ the previous influence of motivation M1 on behaviour. (B) The traditional process of disinhibition (also working in the ADM): motivation M2 increases (here dramatically, but that is not mandatory) and reduces the previous impact of motivation M1 on behaviour. The ADM nevertheless differs from the traditional disinhibition theory in suggesting that inhibition is basically attentional (cognitive) rather than physiological.
quent behaviour through an attentional channel on condition that the former action was of sufficient interest. When the subsequent behaviour is performed, some errors should therefore occur in its execution due to the animal’s distraction. Such a phenomenon is observable in usual activities, as already shown (e.g. Culshaw and Broom, 1980). For instance, two cats meeting in a certain territory often remain immobile and inspect each other. After a time, if nothing has happened, one another may decide to go away. The withdrawal movement is often very slow. This might be to avoid conflict with the other cat—slowness may indicate the former cat’s non-aggressive intention. The ADM is in agreement with this view by suggesting that the moving cat’s abnormal slowness results from the inhibition of its fleeing motivation due to an attentional focus on the other cat.

With respect to displacement activities, the general logic remains identical. Here, I describe what is assumed to happen in food-thwarted domestic hens. Repeated trials allow a hen to learn to go to a place to obtain some food. If the hen does not find the expected food at the next trial, it is said thwarted (or ‘frustrated’) due to the absence of food (Anselle, 1958). As a result, the animal carries out another activity, which is often preening, considered as displacement (e.g. Duncan and Wood-Grush, 1972a,b). The motivation to feed (M1) is here supposed to be of greater intensity than that to preen (M2), as shown in Fig. 5B. However, the preening motivation is probably the only one of which the R-threshold has been reached in this situation. That of the feeding motivation has indeed been raised due to non-food reward: it would be absurd for the hen to continue to behave as if the expected food were there, despite its strong interest in that stimulus. (As reported in Section 5.2, causal factors of R-thresholds are different from those of A-thresholds; R-thresholds are sensitive to environmental influences.) Thinking that the hen’s preoccupation about food is the cause of abnormal patterns observed in preening unfolding is therefore a reasonable hypothesis.

8. Testing the attentional interference hypothesis

Such a hypothesis can be tested. A possible experiment is here briefly described. The fowls of two test groups are subject to a food-deprivation period and learn during repeated trials that some food is available at a given time in their home cage. Just before obtaining their limited daily food, the fowls receive sprayed water on their feathers in order to be disposed to preen. The quantity of water spray is low in a test group and high in the other. The test day, these fowls are food thwarted (no reward available) after receiving water on their feathers and duration of each preening act is recorded—a preening act begins when the fowl’s bill touches a feather and stops when the bill comes away from the feather. The corresponding control groups are subject to the same treatment with respect to water spray but they are neither food deprived nor food thwarted. The test day, the duration of each preening act of control fowls is recorded as well. Adopting a similar definition of the preening act, Duncan and Wood-Grush (1972a) showed that its duration is shorter in food-thwarted fowls than in controls. This abnormally short duration was attributed to the greater ‘frustration’ of food-thwarted fowls. But the psychological significance of that process remains unclear. Disposing the test fowls to preen, as suggested here, might provide a solution to that problem.

The prediction of frustration/anxiety-based models can be contrasted with that of the ADM. According to the frustration/anxiety models, which include Tinbergen’s (1951) overflow model, the thwarted motivation (here, feeding) should affect the duration of preening acts in a similar way, whatever the intensity of the displacement activity’s motivation (preening). The resulting ‘frustration’ or ‘anxiety’ is indeed always the same in the fowls of both test groups since the feeding motivation was identical in each group in terms of deprivation and training. If this category of models makes a correct prediction, a similar decrease in the duration of preening acts should be expected in the two test groups in comparison with the corresponding control groups. Such a prediction means that the influence of frustration/anxiety is equivalent in all test groups, independently of the quantity of water sprayed in the fowls.

According to the ADM, such a result should not appear. The intensity of preening, solicited by water spray on the feathers of fowls, is assumed to raise the A-threshold of the feeding motivation in proportion with the quantity of water sprayed. The more water received by the fowls, the more their feeding motivation should be inhibited. The direct consequence of this process is that attentional interference exerted by the feeding motivation on the preening motivation is more reduced with high water spray than with low water spray. Therefore, the differences between test and control animals in each water spray condition are no longer predicted to be of similar magnitude; these differences attenuate themselves as the quantity of sprayed water increases. Such a prediction means that the influence of attentional interference is reduced when the displacement activity’s motivation is stimulated. In this experiment, neither attention nor anticipation has been evaluated properly speaking. However, confirmation of the ADM’s theoretical prediction would be a strong argument for its principle as it is the sole model to carry out that prediction.

9. The ADM’s solution to unresolved issues

Several problems exhibited by traditional models of displacement activities have been highlighted. I propose here a solution to
Why does the displacement activity not necessarily correspond each of them on the basis of the ADM’s functioning principles. It should appear that the distinction established between motivation and causal factors allows representing attentional interference in a more specific way than with traditional models.

- Why do abnormal patterns appear with motivations of high intensity as well as with motivations of lower intensity?

All models agree that displacement activities occur when the motivations in conflict or thwarted are of high intensity, but none of them can explain why displacement activities are sometimes observed with motivations of low intensity (as reported by Van Iersel and Bol, 1958; Duncan and Wood-Grush, 1972b). Indeed, these models make the assumption that displacements are a consequence of motivational intensity. For the ADM, the important parameter is not motivational intensity but rather the raising rate of A-thresholds between the motivations involved in conflict or thwarting and those involved in displacement. Of course, as already said, if this raising rate is elevated, no interference will be possible between the causal factors of these motivations. But such a scenario must be rejected because it is totally unrealistic; motivational interference does exist. In contrast, if the raising rate is moderate, as represented in Fig. 3, interference will occur in many cases, even though causal factors of the motivations involved are of low intensity. Abnormal patterns are assumed to happen anyway. The reason why displacement activities are essentially reported when the ‘disruptive’ motivations are of high intensity is because they are often observed in critical situations for animals, such as fight and arbitrary reward inaccessibility.

- Why is the occurrence of abnormal patterns related to motivational conflict or thwarting?

Abnormal patterns are pronounced with a strong thwarted motivation (e.g. Zimmerman et al., 2000a), and displacement activities can even sometimes incorporate behavioural elements of the conflicting motivations (e.g. Tinbergen, 1951). Such facts are difficult to understand without hypothesizing that animals continue to pay attention to the object of conflict or thwarting when they perform the displacement activity. Tinbergen’s (1951) overflow model would suggest that motivational ‘energy’ is transferred from one behavioural path to another, but this cannot explain the influence of specific behavioural elements since such ‘energy’ is here supposed to be motivationally non-specific. The ADM considers that attentional interference might be responsible for the expression of abnormal patterns while being able to represent its effect on behaviour. Attentional interference happens when causal factors of at least two motivations overcome their A-threshold; when animals allocate attentional resources to the object of at least two motivations. Carrying out an activity while being distracted by another one is indeed a potential source of errors and inaccuracies explaining why behaviour is sometimes performed faster or slower than usual as well as why behavioural elements can be exchanged between the activities involved.

- Why does the displacement activity not necessarily correspond to an individual’s third motivational priority?

Although disinhibition theories consider that displacement activities correspond to an animal’s third motivational priority, several findings put forward above indicate the contrary (e.g. Witz, 1970; Maestripieri et al., 1992). Such a result is easily understandable if we accept that a motivation and its R-threshold can vary independently of each other. There are indeed good reasons for separating motivational and releasing properties of a stimulus, as suggested by some works in the fields of animal psychology (e.g. Dickinson and Balleine, 1994). For instance, a nutrient is not appetizing in itself for a food-deprived rat; the nutrient only acquires its incentive value once the rat has experienced it under hunger (Balleine, 1992). This means that the rat can act provided that the R-threshold for this nutrient was fixed by experience, independently of the rat’s subsequent motivational state. Other results indicate that the R-threshold’s value of dust-bathing behaviour in fowls varies according to circumstances, such as sunniness, without affecting that behaviour’s motivation (Hogan and Van Boxel, 1993). In these conditions, it becomes possible of imagining a third motivational priority below its R-threshold, because the appropriate stimuli are absent, that is, a third motivational priority unable to express as a displacement activity. In contrast, a fourth motivational priority for which circumstances are more favourable may take its place. For instance, after a fight in monkeys, the self-grooming motivation might be higher than the motivation to be reconciled. But if certain individuals make the circumstances for reconciliation temporarily favourable, the other monkeys may prefer to adopt this latter behaviour. It can be imagined that the monkeys’ self-grooming motivation remains higher than the motivation to be reconciled but that monkeys merely make a strategic choice allowing them to keep their social status. Uncertainty of animals about their social status is indeed suspected to occur after a fight (Maestripieri et al., 1992). In all likelihood, such a scenario should not be the rule, but it needs to be accounted for as a possibility. The ADM allows this possibility to happen.

- Why does a displacement activity only rarely appear without abnormal patterns?

Displacement activities have been often reported as exhibiting abnormal patterns (e.g. Tinbergen, 1951), but sometimes reported as activities without any particularity (e.g. Rowell, 1961). This latter observation was an argument in favour of disinhibition models. Unfortunately, supporters of disinhibition ‘have tended to minimize the importance of any differences that occur’ (Duncan and Wood-Grush, 1972b; see also Roper and Posadas-Andrews, 1981). According to the ADM, the occurrence of abnormal patterns depends on the presence of attentional interference. An absence of abnormalities is thus predicted to arise when attentional interference does not exist. This requires that the displacement activity should be sufficiently motivated in order to raise the A-threshold of the ‘disruptive’ motivations at a higher level of intensity than these motivations themselves, i.e. in order to totally inhibit conflict or thwarting. In all other cases, some abnormalities are expected in the expression of displacement activities. Assuming that the raising rate of A-thresholds is moderate, the ADM is therefore in agreement with the idea that displacement activities exhibit abnormal patterns in a majority of cases.

- Why does the displacement activity not necessarily occur in motivational equilibrium?

Most models consider that displacement activities arise provided that the motivations involved reach equilibrium. However, some empirical findings refute this view (e.g. Kruijt, 1964), which looks like a postulate (Rowell, 1961). In the ADM, motivational equilibrium automatically leads to attentional interference since the reach of such equilibrium requires that causal factors of both motivations overcome their A-threshold. But attentional interference is also possible when conflicting motivations are of unequal intensity. Interference is indeed expected as soon as at least two sets of causal factors have overcome their A-threshold, even though their quantity is different. The ADM therefore sees motivational equilibrium as a particular case of attentional interference, not as a cause of it.

10. Conclusion

Despite obvious scientific enthusiasm about displacement activities over the twentieth century, the origin of their abnor-
nal patterns brought important issues that currently remains unsatisfactorily understood. The ADM is a theoretical alternative considering that traditional models oversimplify the explanation of displacement activities; that the unresolved issues can only find a coherent frame of interpretation within a model that takes into account the influences of multiple variables, such as anticipation, attention, motivation, causal factors of motivation, and reactivity. Some previous models also insist on the role of psychological variables (notably ‘frustration’ and attention) in displacement unfolding, but these variables remain too underdetermined to account for how behaviour can emerge from their interconnections with the postulated motivations. The ADM is an attempt to overcome that theoretical limit and suggests that elementary behaviours as displacement activities require a cognitive explanation in the same way as more complex activities.

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