Some conceptual problems with the classical theory of behaviour

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Abstract

Behaviour is usually assumed to depend on the reach of a critical intensity—termed reactivity threshold—by its motivation. This view represents a simple, predictive theoretical framework in ethology and animal psychology. However, it is here argued that only the influence of an isolated motivation on behaviour can be explained that way; that such a view fails to account for behaviour when several motivations are jointly activated. Upon analysis, the classical theory of behaviour (CTB) proves to be under-specified and thus leads to three conceptual problems that make it logically inconsistent for the study of multiple motivations. A revision of the CTB, called anticipatory dynamics model (ADM), is then developed in order to bring a theoretical solution to these conceptual problems. The ADM hypothesizes that an organism’s motivational interactions are due to the limitation of the organism’s attentional resources.

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1. Introduction

The idea that any behaviour is explicable in terms of a motivational variable and a threshold variable is common in ethology and animal psychology since the works of Seitz (1940, 1941), Lorenz (1950) and Tinbergen (1951), among others. On account of that, this view is here referred to as the classical theory of behaviour (CTB).

In general, the specialists on behaviour decide to study only one activity (e.g. dustbathing, feeding, fighting, diggin) at once in an animal; they presume that this activity is the only one to be motivated at the time they investigate it. The activity’s motivation is usually induced by a deprivation period (e.g. Vestergaard, 1982) or drug administration (e.g. Cooper and van der Hoek, 1993). There is no doubt that the CTB can describe what happens in such situations. But, in nature, things are rarely so straightforward: organisms often want to engage in different activities at the same time, and these activities are not necessarily compatible with each other. For instance, the eggs of herring gulls (Larus argentatus) are incubated in alternation by both parents. The time spent off the nest is devoted to searching for food. Sometimes, one of the two parents is long to come back to the nest because it fails to find any food or is injured. As a result, the incubating bird becomes increasingly hungry. It is then faced with a dilemma: going to feed before its partner returns at the risk that a predator will destroy the eggs, or continue to wait at the risk of being too weakened by hunger to get its food efficiently (McFarland, 1977). I argue that the CTB leads to several conceptual problems that prevent from explaining behaviour in a coherent frame as soon as multiple motivations are involved.

The CTB fails to answer four major questions for behavioural analysis: What is the motivational process of transition from one activity to another? What is the selection criterion of the ongoing activity? What is the criterion that determines the appearance of interference among the activated motivations? And how does this interference affect the ongoing activity? It is shown that the CTB’s conceptual problems are responsible for this failure. A revision of the CTB, called anticipatory dynamics model (ADM), is then put forward to raise its logical incoherencies through an original mechanism. In a nutshell, the ADM takes into account some properties of attention and suggests that an organism’s motivational interactions are determined by the limitation of the organism’s attentional resources.

2. What is motivation?

Before beginning with the topic of this paper, it is important to present the recent literature on the biological bases of animal and human behaviour. As extensively shown since the work of
Olds and Milner (1954), motivational states of organisms are basically physiological. However, the brain mechanisms have some effects at a psychological level (desires, pleasures, aversions, etc.), and it is often difficult to explain why organisms behave as they do without referring to them. The point defended here is that virtually all motivations include both biological and psychological aspects, even in primitive species. This psychological view of motivation should help dissipate some ambiguities about the term motivation as used below, where it is sometimes related to behaviour (ethology), sometimes related to mental states (psychology). In Section 2.1, I describe different brain structures in the light of recent research, and show their involvement in behaviour. Section 2.2 proposes a definition of motivation as a core process merging its ethological and psychological dimensions.

2.1. Neurophysiological control of behaviour

2.1.1. Basal ganglia

Basal ganglia are the most primitive part of the brain since they are directly connected to the spinal cord. They consist in compact groups of neural cells that include the caudate nucleus, globus pallidus, ventral tegmental area, substantia nigra, and striatum—an important output system for higher brain regions concerned with motivation (Rolls, 1999, p. 178). Neurobiological functions located in basal ganglia include those necessary for survival, such as breathing and blood pressure, and for arousal. In addition, these ganglia exert control on the basic behavioural routines of organisms such as elimination, seeking shelter, vocalisation, courtship, and aggressive/submissive displays. Despite their reptilian origin (MacLean, 1973), they continue to influence day-to-day activity cycles in mammals, though, with greater flexibility due to the presence of additional brain structures (see Panksepp, 1998). In humans, diseases affecting basal ganglia lead to deficits in the planning and organisation of everyday activities, ritualistic behaviour patterns such as obsessive-compulsive disorders, and even to irresistible homicidal impulses (reported by Buck, 1999).

Many neurotransmitters are produced in the brainstem. For instance, the cell bodies that produce serotonin (5-HT) are located in midbrain and pontine regions and notably project to the hypothalamus and cortex. Serotonergic systems are involved in arousal, food intake, social interactions, sleep, learning, and aggression. Rats, which normally ignore mice, engage in mouse-killing behaviour when deprived of serotonin by means of certain drugs (Vergnes et al., 1986). And the aggressiveness produced by prolonged social isolation in rats is correlated with a decrease in brain serotonergic activity (Valzelli and Bernasconi, 1979). Serotonin depletion in free-ranking rhesus monkeys living in social colonies brings about aggressive acts directed at inappropriate individuals, such as high-ranking males, increasing their risk of being injured or killed (Mehlman et al., 1994; Higley et al., 1996). Serotonergic systems are highly conserved across evolution and the receptors are so numerous and varied that any clear function cannot be revealed (Kelley, 2005). The most studied neurotransmitter in relation to behaviour is undoubtedly dopamine. It is particularly involved in appe-
areas of the amygdala through the anterior and medial hypothalamus to the lower brainstem where specific behaviours and the physiology of fear are determined. In rats, amygdala damage brings about the loss of conditioned fear (i.e. the startle reflex) in response to a shock-paired sound (Fanselow and Le Doux, 1999). Contrary to the old idea spread by behaviourists that fear is a response to conditioned stimuli preceding pain, there is evidence that both neural circuits are largely dissociated (Bandler and Shipley, 1994). Electrical stimulation of the fear brain system in animals leads them to adopt patterns of behaviour similar to those adopted when confronted with or pursued by a predator (i.e. flight, fight or freeze). However, these typical patterns of fear behaviour are not observed when the classic spinohalamic pain system is activated by electrical stimulation. It should also be noted that rats with amygdala lesions fail to consume salty rewards when physiologically deprived of sodium, even though they exhibit positive hedonic reactions to salty tastes in the mouth (Galaverna et al., 1993). And they fail to work to gain access to a sexual partner, although they engage in copulation if the female is freely available (Everitt, 1990). An explanation for these phenomena might be that amygdala lesions disturb the targeting of motivational/emotional states to particular stimuli, either due to an attentional deficit (Gallagher and Holland, 1994) or due to a deficit in the assignment mechanism of incentive salience to stimuli (Berridge, 1999).

Since the work of Olds (1956), the lateral hypothalamus has been of great interest for the study of motivation. It is indeed located in a continuum running from the ventral tegmental area to the nucleus accumbens—a pathway responsible for anticipation (Robinson and Berridge, 1993) and behavioural facilitation (Depue and Collins, 1999). For instance, neurons of the lateral hypothalamus are stimulated when animals are searching for food, but are shut down as soon as food is found and feeding begins (Hamburg, 1971; Aou et al., 1991). Injuring this part of the brain leads animals to develop aphagia the intensity of which depends on the extent of the lesions (Wong, 2000, p. 99). On the contrary, lesions to the ventro-medial hypothalamus facilitate food intake and engender hyperphagia (Wilkberg and Beatty, 1975). In monkeys, the lateral hypothalamus neurons are aroused by unexpected rewards, but not by fully expected rewards (Schultz, 2000). Despite its major role in the bodily expression of motivation, the hypothalamus can play no executive function. There is evidence that hypothalamic stimulation is motivationally non-specific (Panksepp, 1981). For example, electrical stimulation of the same lateral region allows producing many different consummatory behaviours depending on the animal’s bodily need and environmental context (Valenstein et al., 1970; Berridge and Valenstein, 1991). The hypothalamus depends on higher brain processes as well as on other limbic structures.

### 2.1.3. The prefrontal cortex

The most recent part of the brain, or neocortex, was inherited in neo-mammalian species like primates. It is the top layer of the cerebral hemispheres and is involved in high-level functions, including sensory perception, decision-making, and motor expression—as well as language and thought in humans. At this point I will consider only the prefrontal cortex due to its strong implications for cognitive control of action (Miller, 2000).

The prefrontal cortex is located in front of the brain and represents approximately 33% of the human brain surface. One of its functions is that of extracting information about the regularities across experiences, a process by which rules can be generated to guide cognition and action (Dehaene and Changeux, 1991; Miller, 1999). Another function of the prefrontal cortex is to allow learning of arbitrary associations between sensory cues, motor patterns, and rewards (Petrides, 1985; Gaffan and Harrison, 1988). This region is indeed massively connected with sub-cortical structures (Fuster, 1989), especially with the ventral tegmental area through the mesocortical projection. Dopamine-mediated rewards can then be used as a signal by the brain to guide acquisition of goal-relevant information: the prefrontal cortex neurons react to unexpected rewards, or to cues that predict expected rewards but do not react to the rewards themselves after learning (Schultz et al., 1993). Once elicited in midbrain by an event, dopamine can reach the prefrontal region and activate different populations of neurons that engender cognitive associations. So, after repeated stimulations of these neurons by the same event, associative links could appear and engender connections between this event and the organism’s knowledge (Schultz et al., 1997). Finally, dopamine can maintain activation of some mental representations and thereby protect them against interference from irrelevant sensory information, unless another dopamine influx strengthens another mental representation (Durstewitz et al., 1999, 2000).

According to Damasio (1994), the prefrontal cortex helps organisms to make decisions by associating specific mental representations to emotional states (positive or negative). This is the hypothesis of somatic markers. Doing so, organisms would be prevented from evaluating costs and benefits of each possible action; they could immediately choose the most relevant actions in the situation. There are good reasons for thinking that the prefrontal cortex allows the acquisition of Damasio’s somatic markers. First, the prefrontal cortex is strongly interconnected with virtually all sensory regions where the mental images serving thought are formed as well as with all neural pathways leading to motor responses (Fuster, 1989). Second, it receives signals from important bio-regulatory regions of the brain, such as basal ganglia, amygdala, and hypothalamus. Third, the prefrontal cortex is the place where the events occurring throughout an organism’s life are stored and classified depending on their relevance. This is not to say that the emotions are themselves coded in the prefrontal cortex. Their locations are numerous throughout the brain (Le Doux, 1996). Lesions in the prefrontal cortex do not suppress emotional reactivity but rather prevent learning of the somatic markers (Damasio, 1994). As a result, human patients with such lesions continue to express various emotions in their everyday lives, but are unable to engage in decision-making by appropriately incorporating these emotions to the consequences of their actions.

Although most studies of the prefrontal cortex concern monkeys and humans, other animals, like rats, exhibit prefrontal responses to some events (Berridge, 2003). The prefrontal cortex of rats responds to cocaine and heroin (Chang et al., 1998) and...
these animals work to administer drugs of abuse in that region of the brain (Carlezon and Wise, 1996). Dopamine releases in the prefrontal cortex of rats occur for palatable food or when they are working for it (Richardson and Gratton, 1998) or when detecting a cue that predicts the appearance of unpleasant events like shocks (Davis et al., 1994).

2.2. Defining motivation

It has been shown that motivation is essentially a biological phenomenon, but with such important repercussions at a psychological level that some mental states (desires, aversions, etc.) need to be included in its definition. These mental states are required to explain why organisms behave as they do in their environment. Does this mean that motivation involves consciousness? There is evidence that emotional fever and emotional tachycardia resulting from stressful events—such as handling by human beings—occur in reptiles, birds, and mammals, but are absent in amphibians and fish (for a review, see Cabanac, 2005). These results, as well as others, allow Cabanac (2005) to conclude that only reptiles and more recent vertebrates possess consciousness and its related pleasure/aversion experiences. It is a fact that conscious expression of certain motivational states is required to make behaviour more optimal and subtle—such as moral consciousness, which only appears in primates. But it would be hazardous to consider any psychological description of motivation as involving consciousness. Although pleasure and desire are ordinarily referred to as the subjective experience of conscious states, Berridge (1999) has shown that their core psychological processes can exist without this subjective experience. A photograph of a happy facial expression presented subliminally fails to produce any conscious report of an emotion, but increases a person’s subsequent consumption of a fruit drink, and subjective rating of it, in comparison with a person having subliminally seen an angry face (Berridge and Winkielman, 2003). In other words, pleasure and desire can produce subjective feelings, as suggested by Cabanac (2005), but that is not mandatory. Consciousness is not therefore what basically makes pleasure and desire motivating.

Let’s take another example: anticipation—a process intimately linked to motivation as well. Everybody would agree that anticipation is a psychological state requiring some conscious evaluation of a situation. A typical case of anticipation is that of Pavlovian associations, where a conditioned stimulus (e.g. a sound) is learned to be a predictor of an unconditioned stimulus (e.g. some food): the former allows an animal to anticipate the latter. However, suggesting that Pavlovian associations involve consciousness would be mistaken when one knows that they can be produced in organisms as elementary as paramecia (reported by De Ceccatty, 1962, p. 23). As with pleasure and desire, anticipation is likely to be a core psychological process that can exist in the absence of consciousness.

This debate is therefore a matter of definition. In this paper, I am interested in motivation as a process of variable complexity whose function is to drive behaviour. I do not distinguish between its biological and psychological aspects but rather consider motivation as resulting from a necessary combination of both, even in primitive species (where consciousness does not exist). Similarly, the usual dichotomy between the ethological and psychological approaches to motivation should be avoided: motivation will be sometimes related to behaviour (ethology), sometimes related to mental states, conscious or not conscious (psychology). My view is akin to that of Bindra (1978) that “motivational states influence the production of directed responses, not by a direct influence on motor outflow, but by influencing perceptual processes”: they act on behaviour by making organisms more receptive to relevant stimuli (for recent discussions of the topic, see Balleine, 1992; Anselme, 2006). In this way, all motivations have not only to do with behaviour but also with the mental sphere at different stages. This will appear obvious from Section 6, where our model (ADM) is developed. The literature mentioned below is sometimes old—because multiple motivations have been essentially theorized several decades ago—but the issue is still a topical question.

3. The classical theory of behaviour

Let us take dustbathing behaviour as an illustration of the CTB. This activity is typical of many species of birds and occurs in order to remove excess and stale preening oil on feathers (Van Liere and Bokma, 1987). Dustbathing is essentially determined by deprivation time (Vestergaard, 1982; Vestergaard et al., 1999), substrate quality (Van Liere et al., 1990), temperature (Duncan et al., 1998), and light (Hogan and Van Boxel, 1993). Among these factors, deprivation time has been shown to affect the motivation to dustbathe. In identical light conditions, a fowl is thereby more inclined to dustbathe in the morning, after a one-night break, than in the afternoon because, at that time, the animal’s motivational resources become almost depleted (Hogan and Van Boxel, 1993). Light also increases dustbathing, though by a different mechanism: it does not motivate the bird, but rather seems to decrease the reactivity threshold for that behaviour (Hogan and Van Boxel, 1993). The rate of dustbathing per day (6–18 h) is indeed similar in fowls subject to an extra-light stimulus during one hour (test group) and in fowls placed in normal light conditions (control group). The frequency of that behaviour is merely redistributed in the animals subject to an extra-light stimulus—i.e. when the extra-light stimulus had been presented in the morning, a frequency peak was observed during that time but it didn’t appear about noon as noticed in the animals of the normal light condition. In short, the fowls have similar daily motivational resources at their disposal to dustbathe whatever the light conditions, however, these light conditions also affect the frequency of dustbathing by changing the motivational intensity (or reactivity threshold) required to do so.

The CTB is simple, powerful, and implicitly included in any description of animal and human actions. Its principles have been quite recently restated by Hogan (1997): ‘Such a model [motivation + threshold] provides a general framework for studying and comparing motivational systems across the wide spectrum of systems and species that exist.’ Without going into detail, it is a fact that the CTB makes a number of correct predictions. For instance, it suggests that behaviour does not result from mysterious free will but rather depends on psychobiological
causes; that organisms are all the more disposed to act because their motivation is high (i.e. closer to the reactivity threshold); that the more an organism is motivated to perform an action, the less environmental stimulation is required (Lorenz, 1950); etc.

4. Under-specifications of the CTB

I agree with Hogan (1997) that the CTB is appropriate for studying the impact of a particular motivation on behaviour. Unfortunately, this view might be inappropriate as soon as more than one motivation is activated in an organism—i.e. most of the time. With multiple motivations, the CTB turns out to be under-specified. As shown, it allows (a) two incompatible processes to account for transitions from one activity to another, (b) two incompatible criteria to determine the selection of the ongoing activity, and (c) two criteria to cause motivational interference while being either restrictive or useless (Fig. 1).

Most of these terms can be found in the literature (competition, disinhibition, dominance, and equilibrium), the others are specific to this paper. All describe, however, possible states of motivational systems. The transition processes are usually referred to as competition and disinhibition. Competition means that motivations vary independently of each other, that one motivation may increase without affecting intensity of another. Disinhibition is the reverse process of inhibition; it means that motivations are interdependent, that the decrease in one motivation automatically increases the intensity of another (here, the word intensity indistinctively merges the biological and psychological facets of motivation).

These transition processes explain how one motivation determines the ongoing activity. But they say nothing about the defining criterion of action selection. Two ‘selection’ criteria are distinguished in the literature. On the one hand, dominance of (motivational) intensity means that the stronger motivation is that which originates the ongoing activity. On the other hand, one-threshold reactivity means that the ongoing activity is produced when its motivation is the only one whose intensity has reached its reactivity threshold. Finally, two additional criteria define the appearance of interference among motivations simultaneously activated. The interference criteria are logically complementary of the previous ones. According to equilibrium of (motivational) intensity, some interference appears as soon as at least two motivations become of equal intensity. And multi-threshold reactivity suggests that interference arises when at least two motivations have reached their reactivity threshold.

McFarland and Sibly (1975) thoroughly studied the problem of motivational priorities but, in my view, they are in keeping with the CTB’s logic when they write that ‘it is immaterial from the behavioural viewpoint, whether changes in behaviour are due to attentional or to motor competition’ (see further). Some examples are now used to illustrate the problems encountered within each pair of processes and criteria.

4.1. Incompatibility of the transitions processes

The study of activity transitions (i.e. how to give up an activity for another) has given rise to a vast literature, yet still there is currently no general agreement with respect to the process involved (e.g. McFarland, 1969, 1983; McFarland and Sibly, 1975; Ludlow, 1976; Houston, 1982; Roper and Crossland, 1982; Lester, 1984; Crawford and Colgan, 1989; Hogan, 1989; Freire et al., 1997). Motivations either interact by competition or by disinhibition, but these processes are mutually exclusive. Well, the CTB is not constraining enough to specify which of these processes is the right one, nor whether they coexist somehow. The incompatibility of the transition processes is the first conceptual problem of the CTB to be considered here.

This problem is real insofar as each process can be logically justified. Let us begin with competition. It is admitted that the intensity of a motivation is positively correlated with that of its causal factors. In many studies, motivations are thereby operationally quantified through a measure of their causal factors. For instance, the longer the deprivation of food or water of a rat, the stronger is its hunger or thirst (e.g. Hull, 1943). And the longer the exposure to rivals in a male Cichlid fish, the more the male becomes aggressive (Heiligenberg, 1974). If establishing such a correlation between a particular motivation and the intensity of its causal factors is methodologically relevant, the intensity of any motivation should then be considered independent of that
of the other motivations—assuming that their causal factors are specific. So, an animal that has been deprived of food should continue to be affected by the causal factors of hunger, hence by hunger itself as a motivation, when it is doing another motivated task, such as grooming or fighting. The task carried out is not assumed to reduce the animal’s feeding motivation. In this logic, the process governing motivational interactions is predicted to be competition by the CTB.

Let us now consider disinhibition. In opposition to the principle behind competition, a motivation is here allowed to be of weaker intensity than that of its causal factors. For instance, feeding is suppressed in rats injected with a hypertonic saline solution. Oatley and Toates (1973) measured that each millilitre of water deficit caused by the injection reduced of approximately 0.30 g the quantity of food ingested by the rats. However, such an inhibition of the feeding motivation does not mean that its causal factors decline as well. Inhibition must be thought as a ‘pressure’ phenomenon, like a compressed spring whose natural elasticity makes it usually more extended. Similarly, the rats are still deprived when they decrease their food intake. Persistence of hunger’s causal factors explains the subsequent disinhibition of their feeding motivation. Oatley and Toates (1973) showed thereby that when the rats were allowed to access water, each millilitre of water they absorbed increased of 0.33 g the quantity of food ingested. In this logic, the motivations to feed and drink are assumed to interact in an interdependent way. The process controlling motivational interactions is thus predicted to be (dis)inhibition by the CTB.

In summary, if motivations depend on their causal factors, activity transitions are due to competition. If motivations do not depend on their causal factors, activity transitions are due to disinhibition. As we can see, the incompatibility of the transition processes is caused by the ambiguous relationship predicted by the CTB between motivations and their causal factors. As long as the CTB will not clearly represent this relationship, it will remain under-specified with respect to the process of activity transitions.

4.2. Incompatibility of the selection criteria

It seems reasonable to assume that the ongoing activity in an animal is that whose motivation is the sole to reach its reactivity threshold (one-threshold reactivity). According to Dawkins (1969a), if an animal is performing one activity 80% of its available time and another 20% of that time, this means that the motivation of each activity overcomes its threshold in the same proportions. In contrast, when both motivations reach their threshold within the same bout of time, they interfere with each other and the animal becomes unable to decide what to do. Dawkins’s model is an old one but the principle highlighted is tacitly shared (e.g. Nelson, 1965; ’t Hart, 1985; Hogan, 1997), in addition to being a logical requirement.

In the literature, however, the selection criterion is rarely identified as one-threshold reactivity. It is rather said that the ongoing activity is that whose motivation is the strongest: winner takes all (intensity dominance). No reference to the reactivity threshold is made, as if this was superfluous. For instance, rats accept to cross many times an alley whose temperature is maintained to −15°C when they know that they will find some appetizing food in a warm nest on the other side (Cabanac and Johnson, 1983). But the less appetizing the food, the fewer the rats want to cross the cold alley. If the food is now placed in the cold part of the alley, they go once and no longer return. The contrasting feelings about these two tasks (crossing the cold alley and finding appetizing food) suffice to explain what the rats decide to do. Smooth newts (Triturus vulgaris) court their female on the bottom of a pond, but they frequently need to resurface in order to breathe air (Halliday and Sweatman, 1976; Halliday, 1977). The backward and forward motions of the male newt between its female and the surface of the water indicate alternation in dominance of its sexual and respiratory motivations. As with one-threshold reactivity, the criterion of intensity dominance is in no way arbitrary. The stronger a motivation, the more urgent it is its satisfaction. Since motivations represent an animal’s priorities of action according to their intensity, the criterion can be also viewed as a logical requirement.

Of course, we could imagine that the strongest motivation is necessarily that which reaches its reactivity threshold first, allowing both criteria (one-threshold reactivity and intensity dominance) to be satisfied together—i.e. to be compatible with each other. But this reasoning erroneously presupposes that all reactivity thresholds have the same value for all motivations. Reality is different: as motivations themselves, the value of their threshold varies according to context and learning. Balleine (1992) showed that the reactivity threshold rather than motivation is sensitive to operant (S–R) learning. Rats do not perceive nutrients as rewarding things at start, even though they are hungry. They need to experience them before in order to learn their incentive value. The threshold is then fixed all the lower because the nutrients are good. Once the rats have had their first contact with the food, its attractiveness then remains the same, whatever the subsequent motivation of these animals (for an extended comment, see Anselme, 2006).

Balleine’s (1992) results as well as others (Pelchat et al., 1983; Dickinson and Balleine, 1994; Balleine, 2001; Corbit and Balleine, 2003) support the idea that motivation and its reactivity threshold are two parameters whose numerical values taken over time prove to be uncorrelated. They are governed by different causal factors that make them autonomous in relation to each other. This leads to the second conceptual problem of the CTB: the selection criteria are incompatible in a majority of cases. Either a motivation expresses itself in behaviour because it is the strongest, but nothing ensures us that that motivation has reached its reactivity threshold since this parameter may be higher than that of the other motivations (hence, one-threshold reactivity as a criterion is refuted) or a motivation expresses itself in behaviour because it is the sole beyond its reactivity threshold, but nothing ensures us that that motivation is the strongest since its threshold may be lower than that of the other motivations (hence, intensity dominance as a criterion is refuted).

Fig. 2 illustrates a theoretical example of incompatibility between both selection criteria, which might correspond to the following scenario. After repeated trials, a fowl learns to go to a particular place in order to get its food. If the fowl finds no
food on the next trial, it is said thwarted (or ‘frustrated’) due to the absence of reward (Amsel, 1958). In this case, the animal carries out a substitutive activity, such as preening (Duncan and Wood-Gush, 1972a,b). Preening (M2 in our schema) is much less motivated than feeding (M1) in this situation. However, the fowl’s motivation to preen is likely to be the only one to have reached its reactivity threshold (R2). Indeed, the threshold (R1) of the animal’s motivation to feed had been enhanced due to non-reward: it would make no sense that the fowl continues to behave as if the food was there. Strictly speaking, the CTB does not allow us to predict which selection criterion will work.

How do animals decide to act? Cabanac (1992) has extensively shown that animals tend to maximise pleasure; that they do what they find more pleasant. This is, he says, the way conflicting motivations are resolved. Pleasure is certainly a central component of decision processes and our model (ADM) developed further, which is notably concerned with pleasure anticipation, is in accord with Cabanac’s view. However, I am not quite sure whether pleasure can, in itself, provide a theoretical solution to incompatibility of the selection criteria. To say that greater pleasure determines behaviour is like to say that dominant motivation allows behaviour to happen. But then, the problem described above arises again. A concept of reactivity threshold is needed to explain that, depending on context and learning, a given behaviour is not always released by the same pleasure intensity (see the examples above related to motivation). Well, if the threshold is taken into account, how to be sure that it will allow greater pleasure to determine behaviour in a majority of cases (i.e. that no incompatibility will happen with pleasure as with motivation)? It is true that people sometimes achieve unpleasant activities, such as diets, but there are often secondary benefits at stake that maybe save pleasure maximisation. Considering the reactivity threshold, as an independent variable, calls that principle into question by introducing unpredictable incompatibilities with pleasure. As a result (and in my view), pleasure and motivation are essential to decision-making, but are not specified enough to account for internal conflicts. A way of solving internal conflicts without bringing about incompatibilities is proposed further (from Section 6).

4.3. Limit/uselessness of the interference criteria

What is the criterion determining the appearance of interference among the motivations involved? And how does this interference affect the ongoing activity? It is sometimes suggested that motivations interfere as soon as more than one has reached its reactivity threshold (multi-threshold reactivity). An animal in this situation is indeed logically prevented from doing anything (Dawkins, 1969a). Its behaviour is stalled temporarily or becomes ambivalent, as reported in the case of motivational conflicts (e.g. Tinbergen, 1951), since the animal wants to do several activities simultaneously.

However, multi-threshold reactivity is rarely mentioned as to be the interference criterion. Most works explain the appearance of interference by invoking equilibrium of intensity between the motivations involved (e.g. Tinbergen, 1951; Van Iersel and Bol, 1958; Rowell, 1961; Sevenster, 1961; McFarland, 1966). Equilibrium is presented as the source of motivational interference, which then gives rise to displacement activities because organisms can no longer decide what to do. Displacement activities are banal behaviours of an animal’s repertoire, such as feeding and preening, that suddenly interrupt the ongoing activity when its motivation is interfering with another. They often appear as frantic, incomplete, and of short duration. Writing about the behaviour of a male stickleback (Gasterosteus aculeatus) facing a dummy, Tinbergen (1951, p. 116) reports: ‘after a few minutes the male will attack the dummy again. Just before this happens, however, the male performs displacement digging. This shows, therefore, that displacement digging occurs when the two drives involved are in exact equilibrium.’

Both interference criteria (multi-threshold reactivity and intensity equilibrium) prove to be incompatible with each other since, as with the selection criteria, nothing can guarantee that they will come systematically together. But this problem might not be the right one. The examples taken below suggest (a) that multi-threshold reactivity is necessary but does not circumscribe all cases of motivational interference and (b) that intensity equilibrium is not the cause of motivational interference.

If we admit that motivation and the reactivity threshold are two necessary parameters for the explanation of behaviour (and I do), we must also admit that multi-threshold reactivity leads to motivational interference with important consequences on behavioural expression (sticking, ambivalence). But does multi-threshold reactivity capture all cases of motivational interference? I find it reasonable to believe that a motivation weaker than its reactivity threshold may impede behavioural expression of another motivation whose reactivity threshold has been reached. Imagine a person is doing a task (M1 > R1). The person is also preoccupied and even stressed by an important meeting she must perform the next day. Will she carry out her task serenely? It is probable that the task will be done less efficiently (i.e. maybe slowed down by frequent interruptions or achieved with more errors) than usually because the second motivation interferes with its carrying out. Yet the person’s second motivation cannot have reached its reactivity threshold:
she does not want to go to the meeting at that moment since it is only planned for the next day \( M_2 < R_2 \). This is an example of motivational interference without multi-threshold reactivity.

The same conclusion can be drawn from the example already mentioned of a thwarted fowl that had expected to get food but received nothing. I explained that the fowl’s feeding motivation remained weaker than its threshold—despite its high intensity, because food was not there, while another activity (preening), less strongly motivated, took place. There is evidence that the motivation to feed impedes the expression of the motivation to preen: as a displacement activity, preening is abnormally performed—it is frantic, incomplete, and of short duration—in comparison with the same activity performed in a usual context.

Is intensity equilibrium plausible as an interference criterion? A study by Kruijt (1964) about fighting cocks does not support this idea. A fighting cock (Gallus gallus) is motivated to attack its adversary on the one hand, and to flee from it on the other hand. This antagonism is a cause of motivational interference and engenders displacement activities of different types in the cock (Fig. 3). In particular, Kruijt observed a positive correlation between the displacements produced during a cockfight and the final outcome (winner or loser) for each cock. Winner cocks preferentially expressed their displacement by feeding during the fight, while loser 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 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). Such a result is opposed to the general agreement that motivations interfere in equilibrium. Besides, Rowell (1961) recognizes that equilibrium is a postulate rather than scientific evidence because reliable data are difficult to obtain.

5. Conclusion: how does the CTB account for multiple motivations?

Here is how the CTB answers the four questions asked in the introduction. Important shortcomings may be noticed.

1. What is the motivational process of transition from one activity to another? The CTB cannot decide whether or not motivations strictly depend on their causal factors (competition versus disinhibition). A realistic model of multiple motivations should bring a theoretical solution to this problem.

2. What is the selection criterion of the ongoing activity? Although both selection criteria put forward by the CTB seem justified, they are unlikely to be satisfied together (intensity dominance versus one-threshold reactivity). Since these criteria make sense (i.e. need to be kept), only one of them can therefore turn on action. Then, what is the role of the other?

3. What is the criterion that determines the appearance of interference among the activated motivations? The CTB suggests two interference criteria that reveal, after analysis, either restrictive (multi-threshold reactivity) or useless (intensity equilibrium). If multi-threshold reactivity does not circumscribe all cases of motivational interference, what can the other criterion account for the ‘free-floating’ cases?

4. How does this interference affect the ongoing activity? The consequences of motivational interference on behaviour are varied: immobility, ambivalence, slowing down, execution errors, frenzy, incompleteness, shortness, etc. The CTB does not predict the consequences resulting from multi-threshold reactivity and those that do not.

6. The role of attention and anticipation

The rest of this paper is devoted to develop a theoretical model capable of solving the three conceptual problems of the CTB, that is, a model that explains multiple motivations in a coherent framework. For that, it is argued that such a model must take into account the phenomena of attention and anticipation in organisms—it is referred to as the anticipatory dynamics model (ADM). This statement may seem to be a trivial one insofar as nobody today ignores the role played by cognition in behaviour. However, it is one thing to recognize this idea, it is quite another to show how it can work—in particular for solving our three problems. In general, motivation, attention and anticipation are variables studied separately. These variables are here articulated through a mechanism both simple and potentially applicable to any type of motivational interaction. I specify again that motivation be viewed as a psychobiological process of variable complexity whose function is to drive behaviour. It is then indistinctively defined in relation to behaviour or to mental states without having to think of things of different nature.

6.1. A lacking variable: the anticipatory attention threshold

The CTB’s under-specifications might be removed by introducing a supplementary variable that has certain properties (see
the ADM’s two postulates below): a threshold for the release of the process of anticipatory attention. Organisms pay constant attention to their surroundings, but not systematically with the same ‘depth.’ Most of the time, their attention focuses superficially on this or that object, allowing organisms to recognize it, but such an operation consumes only very little cognitive resources. Recognition is a simple matching between a perceived object and a mental representation of that object. Sometimes, however, organisms find an object of greater interest: this object is then analysed more deeply, consuming much more cognitive resources. Here, organisms are no longer content with recognizing the object, they try to anticipate some information about it—or even try to anticipate the object itself (e.g. some food at a place where it is usually found). By anticipation, I designate the fact of thinking of something absent whose occurrence was expected, or is supposed to happen shortly (maybe due to a given action).

The anticipatory attention threshold is psychologically defined as the ‘demarcation line’ between recognition and anticipation. Straightforwardly, it differentiates attention without allocation of cognitive resources (recognition) from attention with allocation of cognitive resources (anticipation). I admit that such reasoning is oversimplified. Studies in the field of human attention show that recognition also requires allocation of cognitive resources (e.g. Hicks and Marsh, 2000). But I consider that this fact may be ignored for our purpose. As said, organisms are incessantly occupied in recognizing their surroundings. The quantity of cognitive resources devoted to recognition can then be seen as more or less constant over time. Taking it into account within our model is therefore useless. On the other hand, that is different with respect to anticipation: not only are organisms not constantly occupied in anticipating anything, but also the quantity of cognitive resources involved in anticipation is much greater than in recognition. Finally, our anticipatory attention threshold is to be differentiated from the concepts of attention (or ‘liking’) phase of their actions, which rather depends on GABA systems in the brainstem as well as opioid systems in the nucleus accumbens shell (Cromwell and Berridge, 1993; Berridge, 1996; Pecina and Berridge, 1996).

Thus, a massive destruction of ascending dopamine neurons using the neurotoxin 6-OHDA causes profound aphagia in rats (Ungerstedt, 1970; Berridge et al., 1989): the feeding motivation can no longer be stimulated because the rats become unable to anticipate anything pleasant about food. In contrast, these animals continue to like food when they are forced to eat. Depue and Collins (1999) suggest related ideas that dopamine has non-specific action on behaviour but facilitates incentive motivation. For instance, stimulating the dopamine receptors D1, D2, and D3 in the pathway from ventral tegmental area to nucleus accumbens facilitates the acute rewarding effects of stimulants.

However, Sarter and Bruno (1999) think that dopamine does not directly act on behaviour. They report that dopamine release in the nucleus accumbens brings about a greater excitability of cortical cholinergic inputs (see also Himmelheber et al., 2001). These inputs stimulate an organism’s abilities to detect and discriminate sensory stimuli, that is, its attentional capacities. Repeated exposure to cocaine increases acetylcholine release by cortical neurons (Day et al., 1997). In humans, as already noted when opiate users are close to receive drug substitutes like methadone, their reaction time for drug-associated words is shorter than for neutral words in a priming task (Weinstein et al., 1998).

The way acetylcholine is related to attention must be considered cautiously. Inhibition of the GABAergic projections from the nucleus accumbens to the prefrontal cortex is required to allow dopamine to stimulate cholinergic neurons (Moore et al., 1999). But acetylcholine seems unnecessary for attention itself. Passetti et al. (2000) recorded no acetylcholine release with different demands on an attentional task in rats. Acetylcholine might rather discharge because of the expected reinforcement rather than because of the type of action to carry out (Himmelheber et al., 2001).

In a nutshell, dopamine might be essential not only to anticipation but also to attention. I think that this can potentially explain the following contradictory results. Some data indicate that the release of dopamine is observed when an animal must work to obtain cocaine, but not when the animal receives a passive injection (e.g. Dumont et al., 2005). In contrast, other data suggest that cocaine in the ventral tegmental area may stimulate dopamine releases after only one passive injection (e.g. Ungless et al., 2001). The former data, as opposed to the latter, view the impact of dopamine in relation to action. This contradiction might appear illusory, provided that anticipation be taken into account. When the animal is passive and is not expecting a reward, cocaine has no impact on the release of dopamine, since the release of dopamine serves no purpose. When the animal is passive, but finds in a situation where reward may be anticipated, cocaine induces the release of dopamine. Finally, when the animal is ready to act for the reward, cocaine systematically leads to the release of dopamine because any type of action involves anticipation. This is to say that the neuropharmacological effects...
of cocaine might be unrelated to the animal’s ability to act for itself but rather to its ability to anticipate positive or negative reinforcement.

More will be said further, but we can now reasonably suggest two things. First, motivation is narrowly associated with anticipation. In the ADM, the anticipatory attention threshold designates the level zero of a motivation—although it is not necessarily the level zero of the motivation’s causal factors. Second, anticipation stimulates attention by means of dopamine releases. To some extent, this further concretises the abstract concept of anticipatory attention developed here.

6.2. Postulates of the ADM

The ADM relies on two postulates. First, associated with any motivation’s causal factors (F) are a reactivity threshold (R) as well as an anticipatory attention threshold (A), such as the A-threshold always designates a smaller intensity of F than the R-threshold. There is a logical requirement behind this first postulate: in general, the A-threshold needs to be of weaker 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. This can be observed for each F in Fig. 4, which illustrates the second postulate. The second postulate is as follows: when a motivation’s causal factors overcome their anticipatory attention threshold, this raises the reactivity threshold of concurrent causal factors. To understand this idea, a few words must be said about the limited attentional resources of organisms.

The more an organism’s attention toward an object, the less the organism can allocate its attention to another object in the same period of time. This is to say that an organism’s attention can hardly be paid to more than one object at a time without bringing about interference. In humans, it has been extensively shown that sharing one’s attention on two tasks leads to a decrease in performance in comparison with the same tasks carried out separately. Reaction times are slowed down, more errors are significantly made, etc. (e.g. Noble et al., 1981; Hirst and Kalmar, 1987; Baddeley, 1990). This phenomenon is also known in animals and has been especially studied in pigeons (see Robbins, 1998; Lejeune et al., 1999; Zentall, 2005). For instance, a stimulus is presented to pigeons and followed by a choice between two comparison stimuli. The initial stimulus is either simple (composed of one feature) or complex (composed of two features) while the comparison stimuli are composed of only one feature. This feature matches a feature previously seen in only one of the two comparison stimuli. It is observed that pigeons do fewer comparison errors to process one-featured than two-featured initial stimuli (e.g. Maki and Leith, 1973; Zentall et al., 1997). After many experimental tests, it has become obvious that when there is limited access to the discriminative stimuli (the duration of the sample is limited), the animals must either attend to one dimension at a time or they must divide or share their limited attentional capacity between the two dimensions (Zentall, 2005). In animals as well as in humans, an extensive training is able to improve performance, but interference can never be totally eliminated (Zentall et al., 1997; Shallice et al., 1985).

Thus, Fig. 4 must be understood as follows. On left part the causal factors of three motivations are considered. F1 are not ‘converted’ into motivation because they remain under their A-threshold (F1 < A1). F2 are ‘converted’ into motivation (M2) since they are above their A-threshold (F2 > A2). F3 are absent—hence no motivation either. So, an organism with such internal states would exclusively pay anticipatory attention to some information about the object of M2. Such a configuration is due to the organism’s attentional limitation: M2 has raised the A-threshold of F1 and F3. Indeed, the attentional resources allocated to the object of M2 can be no longer allocated to the object of other causal factors—a process represented by the dynamics of their A-threshold. Here, F1 and F3 might motivate the organism as well, but on condition to become of higher intensity than that prescribed by their respective A-threshold. Taking into account here the first postulate, we understand why the R-threshold of F1 and F3 are raised; it is raised in order to remain of higher intensity than their respective A-threshold. As said, this is a logical requirement preventing the organism from acting before wanting to do it. On the right part, it is supposed that F1 strongly increase till overcoming their A- and R-thresholds. F1 are therefore partially ‘converted’ into motivation (M1). As a result, this strongly raises the A-threshold of F2 and F3, bringing about a raise in their R-threshold as well. It can be observed that the organism’s attentional limitation here causes total inhibition of M2, that is, the temporarily inability of anticipating anything about its object, despite the presence of specific causal factors F2. Maintained like this, F2 will probably collapse.

6.3. Illustrations of the anticipatory dynamics

6.3.1. Example 1: distraction of an aggressive dog

A dog may become aggressive when confronted with something unknown on its territory, such as a hedgehog in the garden. It may vigorously bark at it while exhibiting a threatening attitude (bared teeth, bristled coat, flattened ears, etc.). However, if the dog’s attention is suddenly diverted by another stimulus (e.g. the dog is called by its master), its threatening attitude is reduced or even stopped a few instants: there is (partial or total) inhibition of the dog’s aggressiveness. Does this mean that the causal factors of its aggressiveness disappeared? Is it a matter of competition? This is what the CTB might suggest. But such a view is hardly credible. The dog is able to maintain a representation of the intruder in its memory. Thanks to the hedgehog representa-
intake dramatically increased. The rats were then deprived of d-than group-housed ones (Wolffgramm and Heyne, 1995; Heyne, nant ones, and socially isolated animals consumed more drug on social hierarchy: subordinate rats drank more than domi-
was observed that the quantity of drug they absorbed depended (Vanderschuren and Everitt, 2005). For instance, in rats hav-
6.3.2. Example 2: compulsive drug seeking
When rats are allowed to self-administer cocaine during a prolonged period, they absorb increasing doses of that drug (Ahmed and Koob, 1998). Then, if these rats are subject to a withdrawal period, they adopt cocaine-seeking behaviour whose intensity is related to the withdrawal period length (Grimm et al., 2001). Compulsive drug seeking is operationally defined as ‘continuation of drug seeking and taking despite aversive consequences, despite obvious and detectable decreases in the subjective value of the drug (devaluation), or as being insensitive to internal and external manipulations (‘inflexibility’)’ (Vanderschuren and Everitt, 2005). For instance, in rats hav-
Fig. 5. (A) The dog is aggressive and pays only attention to an intruder on its territory. This motivation (M1) raises the A- and R-thresholds of any other potential motivation. (B) The dog is distracted by a second stimulus, inducing motivation M2, so that the A- and R-thresholds of its aggressive motivation are raised, in turn. This causes the inhibition of the dog’s aggressive motivation as well as of its threat attitude (inhibition is here important but not total).

amphetamine for a period of 1–6 months. Once they re-obtained their drug, intake could no longer be modulated, as before, by social factors nor even by gustatory factors (drug taste was devalued with quinine).

Behavioural disorganisation of rats is a consequence of withdrawal symptoms. These symptoms include the pathological attentional focalisation of rats on the rewarding properties of cocaine. As said, dopamine levels in the nucleus accumbens determines how much a drug is wanted (Robinson and Berridge, 2000), and they lead to a disinhibition in the excitability of cortical cholinergic neurons, involved in attention (Sarter and Bruno, 1999). Therefore, ‘Deficits in the ability to filter irrelevant stim-
ules and higher processes […] are attributed to pathological increases in the activity of cortical cholinergic inputs.’ (Sarter and Bruno, 1999). In fact, dopamine might be necessary to cholinergic neuron firings. Himmelheber et al. (2001) unexpectedly observed that increasing or decreasing explicit demands on an attentional task in rats were not associated with fluctuations in frontoparietal acetylcholine efflux. Significant releases only appeared as soon as the rats were transferred to the operant cham-
ber, despite their extensive experience with the transfer protocol. Although more experimental investigations are here required, Himmelheber et al. (2001) consider that anticipation of reinforcement might explain the excitation of cholinergic neurons. Anticipation of a palatable meal was indeed shown to stimulate acetylcholine efflux in hippocampus and cortex (Inglis et al., 1994).

Why does an organism exhibiting severe withdrawal symp-
toms give up its usual activities and try to obtain a drug at all costs? In fact, obsessive drug seeking can be also observed in non-deprived animals, that is, in individuals without withdrawal symptoms. The ADM can both explain the inhibition of these activities as well as the observed inflexibility of drug seeking (Fig. 6). According to the ADM, the strong addictive moti-
vation of organisms causes intense anticipation about—hence, intense attentional focalisation on—the rewarding properties of cocaine. Owing to limited resources of attention, this leads to dramatic raise of the A- and R-thresholds of any other motivation. Even though the rats have been food deprived, the causal factors of hunger can no longer be ‘converted’ into motivation. These causal factors are unable to make the organism hungry as long as they remain below the intensity prescribed by their raised A-threshold. This means that the rats are able to recognize food but do not want to eat, because no pleasure is expected from the food. In sum, the inhibition of any motivation not drug-directed is here total, bringing about a series of negative consequences, of which sometimes the organism’s death.

7. A mathematical framework for anticipatory dynamics
The ADM can be formalised through a set of simple equations. This formalisation describes the mechanism responsible for motivational interactions in our viewpoint, although the exact values of parameters must be determined by appropriate experiments. The formalism presented below is of purely theoretical interest in this paper.
7.1. Motivation interval \( \mu \)

It has been suggested that a motivation’s causal factors allow organisms to anticipate—or to allocate attentional resources—about their object provided that they reach their A-threshold. Thus motivation only corresponds to the part of intensity of its causal factors beyond their A-threshold. For an isolated motivation, such a distinction makes sense with motivations whose A-threshold has been raised. This contrasts with the CTB, which does not represent the causal factors of motivations, and will prove to be necessary for solving the CTB’s first conceptual problem. A motivational interval, \( \mu \), is then calculable once the intensity of a motivation’s causal factors is known as well as the value of their A-threshold (Eq. (1)):

\[
\mu_i = d_i - a_i
\]

where \( \mu_i \) is the motivational interval of given causal factors, \( d_i \) the intensity of the motivation’s causal factors, and \( a_i \) the intensity of their A-threshold. The value \( \mu_i \) reaches its maximum with an isolated motivation of maximal intensity. This particular case is likely to be rare, but not impossible. It might correspond to what happens in withdrawal symptoms, which lead to compulsive drug seeking, because \( d_i \) is maximal and \( a_i \) is zero. Now the value \( \mu_i \) reaches its minimum in the opposite case: the causal factors of a motivation are equal to zero while another motivation of great intensity is activated. Here, \( d_i \) is zero and \( a_i \) is maximal. As long as \( \mu_i \) is negative or null (\( \mu_i \leq 0 \)), the organism is non-motivated by the causal factors involved, that is, unable to anticipate anything about their object. These causal factors cannot therefore affect the A-threshold of any other motivation’s causal factors.

7.2. Variations of A-thresholds

The A-threshold value of a motivation \( M_1 \) is raised by an increasing motivation \( M_2 \). This is the process of \( M_1 \) inhibition. It means that an organism becomes less motivated about the object of \( M_1 \) as \( M_2 \) increases because of its attentional limitation. Conversely, the A-threshold value of \( M_1 \) is lowered by a decreasing \( M_2 \), leading to \( M_1 \) disinhibition. The organism then becomes more motivated about the object of \( M_1 \) as \( M_2 \) decreases. In a nutshell, anticipatory dynamics may be conceptualised as communicating vessels. Formally speaking, however, motivational interactions are more complex in that the effect of the distinction between a motivation and its causal factors must appear in the dynamics. Indeed, the dynamics of A-thresholds does only work assuming that the increasing/decreasing causal factors are ‘converted’ into motivation. As said, when a motivation’s causal factors fluctuate below their own A-threshold, they have no incidence on any A-threshold.

Two rules stem logically from previous analysis. First, any increase in a motivation’s causal factors whose final intensity goes beyond their A-threshold raises the A-threshold of concurrent causal factors as follows:

If \( d_1 + k \),

then \( a_{2*} = a_2 + tk \quad (d_1 \geq a_1) \) (2)

or \( a_{2*} = a_2 + (k + \mu_1) \quad (d_1 < a_1 < d_1 + k) \) (3)

where \( d_1 \) designates the intensity of a motivation’s causal factors, \( k \) the value they are increased at a given time, \( a_2 \) the A-threshold value of another motivation’s causal factors before being raised, and \( t \) the rate with which \( a_2 \) is to be raised. The value \( a_{2*} \) symbolises \( a_2 \) after being raised. The equations above are instantiated by numerical values below (see also Fig. 7). Let us remark that the value \( t \) is assuredly null or positive for all motivational inter-
actions, though, not necessarily identical in every case. In my opinion, $t$ can never be too high (except maybe with addictive substances) because then motivational interference (e.g. doing a task while focusing one’s attention on something else) would be impossible. Well, the occurrence of conflicts of interests is frequent in the animal kingdom. In the Eq. (2), for instance, $A_1(a_2, a_2^* < k$ if and only if $t < 1$. Nevertheless, $t$ might be very different from one motivational interaction to another. It might be reasonably suspected that a high-priority motivation, such as attacking, brings about stronger A-threshold raises of low-priority motivations (e.g. preening) than of other high-priority motivations (e.g. feeding). Conversely, a low-priority motivation should cause stronger A-threshold raises of other low-priority motivations (e.g. digging) than of high-priority motivations. Without such a hypothesis, not only would low-priority motivations have great difficulty in expressing themselves in behaviour, but also high-priority motivations would be incessantly impeded by peripheral activities.

Why are two equations necessary to explain the A-threshold raises? According to the ADM, the A-threshold value $a_2$ can only change provided that the causal factors $d_1$ have already reached their A-threshold value, noted $a_1$. It must then be distinguished whether $d_1 > a_1$ already before its increase $k$ ($\mu_1$ is always positive) or whether $d_1 < a_1$ before its increase $k$ ($\mu_1$ starts negative but is smaller than $k$). In the first case, the Eq. (2) is used (Fig. 7A). Let us consider a theoretical example in which $d_1 = 0.3, \mu_1 = 0.3, t = 7/10$ and $a_2 = 0.2$. The raised value of $a_2$ becomes $a_2^* = 0.2 + (7 \times 0.3)/10 = 0.41$. On the contrary, if $d_1$ begins its increase when still below $a_1$ and $|\mu_1| < k$, the raise of $a_2$ is then smaller because $d_1$ increases in part while inducing no change in $a_2$. The Eq. (3) needs to be applied (Fig. 7B). With $\mu_1 = -0.1$, the new value of $a_2$ becomes $a_2^* = 0.2 + 7(0.3 + (-0.1))/10 = 0.34$.

The second rule characterising the ADM suggests that any decrease in a motivation’s causal factors whose initial intensity overcomes their A-threshold lowers the A-threshold of concurrent causal factors as follows:

$$\text{If} \quad d_1 - k,$$

then $a_{2e} = a_2 - tk \quad (d_1 - k \geq a_1)$ \hspace{1cm} (4)

or $a_{2e} = a_2 - t\mu_1 \quad (d_1 - k < a_1 < d_1)$ \hspace{1cm} (5)

The same logic has to be applied here. Two equations are necessary to account for $a_{2e}$ depending on whether $d_1 > a_1$ after its decrease $k$ ($\mu_1$ is always positive) or whether $d_1 < a_1$ after its decrease $k$ ($\mu_1$ starts positive but is smaller than $k$). The Eq. (4) is used in the first case (Fig. 8A). Let us take $k = 0.3, t = 7/10$, and $a_2 = 0.5$. The lowered value of $a_2$ becomes $a_{2e} = 0.5 - (7 \times 0.3)/10 = 0.29$. However, if the intensity $d_1 - k$ goes below $a_1$ (i.e. $\mu_1 - k$ is negative), the lowering of $a_2$ is then smaller because $d_1$ decreased in part while inducing no change in $a_2$. The Eq. (5) is required (Fig. 8B). With $\mu_1 = 0.2$, the new value of $a_2$ becomes $a_{2e} = 0.5 - (7 \times 0.2)/10 = 0.36$.

All these results are worthless as such—because they rely on parameters whose numerical values have been arbitrarily chosen. But the equations themselves describe the process of anticipatory dynamics. Of course, the logic behind these equations can be applied to as many motivations as we need to consider. But the ADM predicts that the more motivations involved, the less interference is possible among them. Indeed, the A-thresholds become higher and higher as the number of motivations increases. It is then more difficult for their causal factors to remain beyond their A-threshold. This might explain why, in nature, motivational interferences are reported to involve no more than two or three motivations.

8. Solutions to the CTB’s conceptual problems

Four major questions related to multiple motivations have been highlighted in this article’s introduction and it was mentioned, in Section 5, why the CTB unsatisfactorily answered them. By way of conclusion, I suggest reconsidering here these questions in the light of the ADM in order to eliminate the CTB’s logical incoherencies.

1. What is the motivational process of transition from one activity to another? The CTB hesitated between competition and disinhibition because it was unclear about how motivations interact with their causal factors. According to the ADM, the causal factors of motivations do not depend on each other; they interact by competition. On the contrary, motivations themselves never interact that way. The attentional limitation of organisms makes them interdependent: they interact by inhibition or disinhibition. Thus, the ADM predicts that an isolated motivation is strictly determined by the intensity of its causal factors, whereas multiple motivations are of reduced intensity in relation to their causal factors. Thanks to the dynamical nature of A-thresholds, both transition processes become compatible with each other.

2. What is the selection criterion of the ongoing activity? For the CTB, action selection was associated with two incompatible criteria: one-threshold reactivity and intensity dominance. The ADM recognizes the conceptual relevance of both these criteria but considers that they are not selective in the same way. One-threshold reactivity is about action selection and means that only one motivation has reached its R-threshold. Intensity dominance is related to the selection of attentional resources and happens when one motivation overcomes its
A-threshold with stronger intensity than the others—even though none has reached its R-threshold. Both selection criteria are here no longer incompatible insofar as they turn on different things.

3. What is the criterion that determines the appearance of interference among the activated motivations? Beyond their incompatibility, the CTB’s interference criteria presented additional difficulties. Multi-threshold reactivity revealed restrictive and intensity equilibrium useless. It was then asked what is the interference criterion for the cases not accounted for by multi-threshold reactivity? The ADM distinguishes two types of interference. The first type, called behavioural interference, arises with multi-threshold reactivity, as predicted by the CTB. The second type, called attentional interference, arises when the causal factors of at least two motivations have reached their A-threshold. Thus, the ADM allows understanding why a motivation below its R-threshold can impede the expression of another. All cases of interference are thereby circumscribed without engendering conceptual incompatibilities since the behavioural and attentional types of interference turn on different things.

4. How does this interference affect the ongoing activity? The CTB considered interference in strictly behavioural terms despite the great variety of its exhibition (e.g. sticking, ambivalence, slowing down, execution errors, frenzy, incompleteness, shortness, etc.). Insofar as the ADM predicts two types of interference, their consequences are differentiated. Behavioural interference should give rise to sticking or ambivalent actions, as often observed in attack-flee conflicts. In contrast, attentional interference should rather modulate the speed of action (slowing down or frenzy), as well as bringing about errors and incorrectness in the action unfolding. Such patterns typically occur in thwarting situations, as noticed above.

The ADM is a theoretical framework designed to suppress the logical incoherencies of the CTB. Its relevance for the study of animal and human behaviour currently remains hypothetical. The model now needs to be empirically tested through adequate experiments. Several should be shortly run in this aim.

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References