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Two modes of input processing in relation to sperm competition in mammals *

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Abstract Much research has been focused on the 'output' or response of males to particular risks of sperm competition（RSC）. Lately，there has also been some interest on the types of information that males may use to assess RSC（RSC inputs）. In contrast，there is a lack of studies on how males may process RSC inputs to generate such RSC outputs. Here we propose two modes of *input processing*（direct and indirect）and ways to test them in order to understand how a male may process and store RSC information. The direct mode of input processing predicts that a male may store RSC inputs through a physiological response，e.g.，through a change in hormonal levels. As long as this response is active，the male will stay in a 'RSC state' and will produce an RSC output（e.g.， high sperm investment）instead of a non-RSC output（e.g.，relatively lower sperm investment）when he encounters a female. The indirect mode of input processing predicts that a male may store RSC inputs in his memory and retrieve such information later on to modify his output（e.g.，sperm investment or copulatory behavior）accordingly. We use a multidisciplinary approach that should appeal to those researchers that seek to understand male's adaptations to sperm competition at different levels. We believe that the testing of the hypotheses developed in this paper will lead to interesting findings and the development of new hypotheses［*Acta Zoologica Sinica* 51（6）：1122－1129，2005］.

Key words Sperm competition intensity and risk，Hormones，Memory，Copulatory behavior，Brain

与哺乳动物精子竞争有关的两种信息输入处理模式 *

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摘　要　过去的许多研究集中在“输出”或雄性对特定的精子竞争风险（Risks of sperm competition，RSC）的反应上，对于雄性利用何种类型的信息来估计RSC也有一些研究。相比而言，缺少对于雄性如何处理RSC信息输入从而产生RSC信息输出的研究。本文提出输入信息处理（直接处理与间接处理）的两种模型并提出了检验这两种模型的方法，以便理解雄性如何处理并储存精子竞争风险的有关信息。直接的输入信息处理模型预测，一个雄性个体可能通过生理反应如激素水平的变化来储存RSC的输入信息。只要这种反应处于活动状态，那么雄性个体将处于“精子竞争风险状态”并产生RSC输出（例如，高精子投资）而不是处于非精子竞争输出状态（例如，相对低的精子投资）。间接的输入信息处理模型预测，雄性个体可能在它的记忆中储存与RSC相关的的输入信息，并在其后使用这些信息以调节其输出（例如，精子投资或交配行为）。我们使用能吸引研究者的多学科方法以理解雄性在不同层次对精子竞争的适应，相信对本文提出假说的检验将有助于新的发现以及新假说的发展［动物学报 51（6）：1122－1129，2005］。

关键词　精子竞争强度和风险　激素　记忆　交配行为　脑

Sperm competition takes place when the sperm deposited by two or more males compete within the reproductive tract of a given female to fertilize her egg/s（Birkhead and Møller，1998；Parker，1970）. Sperm competition is widespread across animal taxa（Birkhead and Møller，1992；Birkhead and Møller，1998；Dewsbury，1984；Ginsberg and Huck，1989；Radwan，1991；Simmons，2001）. In many species，the regular occurrence of sperm competition has produced physiological，morphological，and behavioral

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adaptations in both males and females. For example, in species where sperm competition is common, males have relatively larger testes than do males from species in which sperm competition is rare (Byrne et al., 2002; Harvey and Harcourt, 1984; Møller, 1988; Stockley et al., 1997). Also, at the individual level, males may increase their sperm investment (total number of sperm allocated by a male to a particular female) in response to a risk of sperm competition (RSC) (Candolin and Reynolds, 2002; Gage, 1991; Pilastro et al., 2002; Pizzari et al., 2003; Wedell and Cook, 1999). For example, male meadow voles *Microtus pennsylvanicus* increase their sperm investment when exposed to the odors of a conspecific male (delBarco-Trillo and Ferkin, 2004), and male rats *Rattus norvegicus* show the same response in the presence of a conspecific male behind a partition (Pound and Gage, 2004). This type of modulated response (e.g., adjusting sperm investment in response to different RSC) may be categorized as the 'output' of a male (Fig.1).

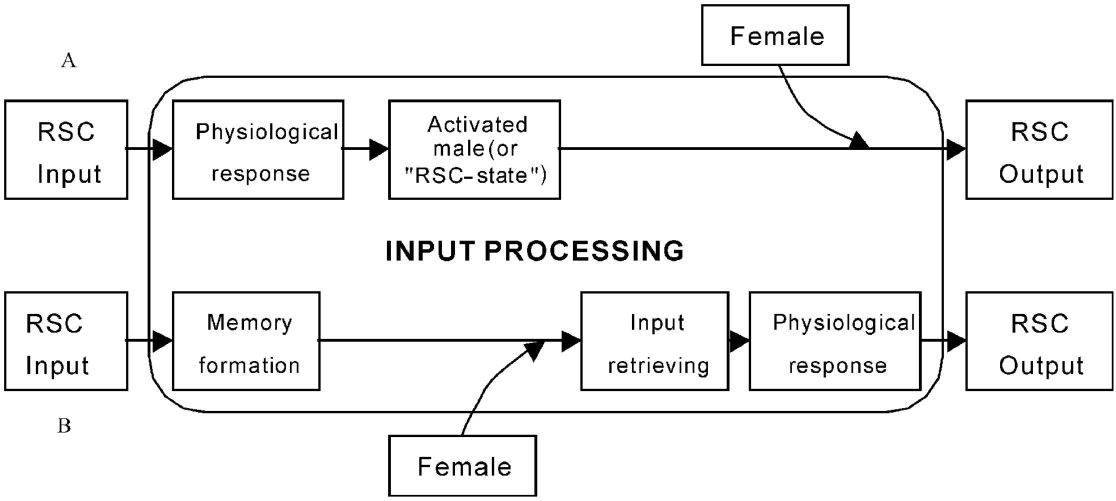

Fig.1 Schematic representation of the two modes of risk of sperm competition (RSC) input processing described in the text

The rounded rectangle represents the processing of the input prior to the generation of the output. A. Direct processing. A male processes the RSC input by generating an immediate physiological response. As long as this response is effective, the male is ready (or 'activated') to produce an RSC output that is in accordance with the RSC input that 'activated him'. B. Indirect processing. A male processes the RSC input by forming a memory of that input. When it is time to produce the output, this memory may be retrieved to generate a physiological response that will affect the intensity or quality of the output. By output, we refer not only to sperm investment, but also to behavioral responses, such as mate guarding and copulatory behavior (Stockley and Preston, 2004). See text for a more detailed description of both modes of input processing.

Most research on sperm competition at the individual level has been focused on the male's output, mainly measuring variables associated with sperm investment (Gage, 1991; Wedell and Cook, 1999) and copulatory behavior (Candolin and Reynolds, 2002; Hogg, 1988). Also, there have been some studies on the physiological mechanisms underlying the control of sperm investment in relation to RSC (Anderson et al., 2004; Pound, 1999). The extensive research on the output in response to RSC contrasts with the scarcity of research on the nature of the input, and especially on the processing of that input to generate an output. By 'input' we refer to the information that males may use to assess RSC (delBarco-Trillo and Ferkin, 2004). Presently, we know that males may use olfactory, auditory and visual cues to assess RSC (delBarco-Trillo and Ferkin, 2004; Dewsbury, 1984; Ginsberg and Huck, 1989). More research is still needed to expand the list of inputs that males may use to assess RSC. In this regard, it is important to realize that the inputs used by any particular species will depend on the sensory capabilities of that species. In addition, an individual male may use multiple types or combinations of inputs to assess a single RSC event and generate a similar output.

'Input processing' in relation to RSC refers to the physiological and/or cognitive mechanisms linking the reception of RSC inputs and the delivery of an RSC output (Fig.1). The present paper is the first effort to address the 'input processing' in relation to RSC by considering how males may store RSC inputs, especially when there is a temporal delay between the reception of RSC inputs and the delivery of an RSC output. In most studies that have investigated changes in male output in response to a RSC input, the male delivered his output while being exposed to the RSC input (delBarco-Trillo and Ferkin, 2004; Pound and Gage, 2004). In natural settings, however, this may not necessarily be the case. Both the time and place of exposure to RSC inputs may be different from the time and place of output delivery. For example, a male may encounter odors of other sexually active males somewhere in a territory before he encounters a sexually receptive female and copulates with her elsewhere in that territory (Gosling and Roberts, 2001). Males may therefore have the ability to store and update RSC inputs to be able to modify their outputs later on. It is when we consider a delay between the RSC input and the RSC output that addressing the processing of RSC inputs becomes the most relevant.

We introduce two possible modes (direct and indirect) of processing and storing of RSC inputs (Fig. 1). In the direct processing, males respond in a stimulus-response fashion. That is, exposure to the stimulus (RSC input) elicits an automatic and direct response, e.g., a particular hormonal release. As long as this response is maintained, the male will be 'activated to respond' and, when encountering a female, he will produce an RSC output. When the response attenuates (for the previous example, when the released hormones return to baseline levels) the male will stop being 'activated to respond' and he will deliver a non-RSC output (i.e., as if the male had not been exposed to a RSC input). In the indirect processing, the male stores the information about the RSC input in his memory, and when it is time to deliver the output the male retrieves that information from his memory to modify his output accordingly (i.e., by delivering an RSC output).

We will develop both modes of input processing with a focus on mammals. Although some of the generalities of both processing modes may be applied to other groups of organisms, the physiological and cognitive underlying mechanisms in mammals may be substantially different to those in other groups. Additionally, we will focus on how males process and respond to SCR inputs without considering the role of the female. Future considerations may be focused on how females may manipulate the perception of RSC inputs by males (Garamszegi et al., 2005).

For both modes of input processing, we will describe how males may respond differently to a RSC input than to a non-RSC input. In doing so, we are not suggesting that RSC is a binary variable (i.e., either present or absent). While sperm competition itself may be present or absent (thus a binary variable), the risk of its occurrence (RSC) is a continuous variable, ranging from certainly absent to certainly present (Parker et al., 1997). Similarly, the response of a male to a RSC (i.e., his RSC output) will generally be continuous (both sperm investment and most copulatory behavior variables are continuous variables). However, even though the quantitative response of a male to particular RSCs may vary depending on lower or higher risks (Parker et al., 1997), the qualitative response beyond a given threshold of RSC may generally be the same (e.g., a significant increase in sperm investment or frequency of ejaculations in relation to a control context). In an effort to make the two modes of input processing easily understandable, we consider a RSC input as such when it triggers a measurable change in the output of a male (RSC output). More complexity may be introduced in both processing modes by considering different degrees of risk of sperm competition and the according modulations of the RSC output.

Another issue that should receive future consideration involves intraspecific differences among males. Different males may process the same RSC input differently depending on their own status (e.g., dominant/subdominant males). In addition, signs of competing males may convey different information to a focal male depending on the condition of those males. For example, a male red deer may experience a higher risk of sperm competition when detecting another male with large antlers (trait correlated with testes size and sperm quality) than when detecting another male with smaller antlers (Malo et al., 2005).

1 Two modes of input processing

Although the direct mode of input processing involves primarily an immediate physiological response, and the indirect mode involves cognitive processing and storage of information, both modes are necessarily connected. If we broadly consider cognition as encompassing mechanisms from signal perception to internal representation and memory, cognition will be always involved in any type of sexual behavior (Domjan, 2002; Godfrey-Smith, 2002), including any male response to RSC. Similarly, any processing of information in relation to RSC will ultimately require a physiological response mediated by hormonal and neuroendocrine processes (Domjan, 2002). Therefore, the two modes of input processing are not mutually exclusive. However, there are two reasons to initially address each processing mode separately. First, this will facilitate the study of what it is undoubtedly a very complex series of physiological and cognitive processes. Second, separating physiological and cognitive processes will facilitate research on this new area of study, because reproductive physiologists, behavioral ecologists, neurophysiologists, and cognitive psychologists may separately address questions and hypotheses within their respective fields and at different levels of analysis (Kamil, 1998). Obviously, there are multiple possibilities to address either of the two modes of input processing from a multidisciplinary perspective.

1.1 Direct mode of input processing

The first mode of input processing involves a direct physiological response when the male is exposed to a RSC input (Fig.1A). This physiological response may have an effect on the output immediately (or in a question of seconds), or a relatively delayed effect if there is a cascade of events before the output can be modified. For example, a particular RSC input may elicit a release of LH (Luteinizing hormone), which subsequently would stimulate an increase in testosterone levels, which may have different effects in the male's output. The main idea in the direct mode of input processing is that, after detecting a stimulus containing RSC information, the male experiences a physiological response, which elicits a 'RSC state' (Fig.1A). A male in the 'RSC state' is physiologically different from he was before encountering the RSC input. As long as the male stays in this 'RSC state', the male will be 'activated' to produce an output in accordance with the RSC input that 'activated him' (Fig.1A). That is, if a male copulates with a female while he is in a 'RSC state', an RSC output will be activated rather than a non-RSC output. The 'RSC state' will eventually be lost when the physiological factor (or factors) that elicited the 'RSC state' attenuates and returns to baseline levels. At this point, the male should behave as if he had not initially detected the RSC input, i.e., by delivering a non-RSC output. This response may be adaptive, because if a male does not detect RSC inputs over a given period of time, the RSC will in fact have decreased significantly and a non-RSC output may be more appropriate than an RSC output.

When a male is in the 'RSC state', there are two possible mechanisms by which that 'RSC state' may be translated into an RSC output. First, there can be a discrete yes/no type of response, in which there will be a consistent RSC output as long as the male stays 'activated' (or in the 'RSC state'). This means that the initial and final periods of any 'RSC state' will be functionally equivalent. This yes/no type of response may take place if there is a physiological threshold determining whether the RSC output is produced or not. Second, there can be a modulated or graded response if the intensity of the RSC output depends on the intensity of the 'RSC state'. For example, the factor (hormone, neurotransmitter, receptor activity, etc.) that promotes the 'RSC state' may reach a peak soon after the male encounters the RSC input, followed by a gradual decline back to baseline levels. If so, the highest RSC output would be delivered when the physiological factor is peaking while lower RSC outputs may be delivered as that factor declines.

1.2 Indirect mode of input processing

In the indirect mode of input processing, the RSC input is first processed and stored in the male's memory (Fig.1B). Later, when the male encounters a receptive female and copulates with her, the information encoded in the memory of the male will be retrieved to modify his output accordingly. Therefore, in the indirect model there are three cognitive mechanisms (processing, storage, and recall of information) that connect the input and output (Yoerg, 1991). Between input reception and output delivery the male is not 'activated' to respond immediately with an RSC output as he was in the direct mode of input processing. Rather, only when it is time to produce the output will the information stored in the male's memory be retrieved and will the male enter a 'RSC state' enabling the immediate delivery of an RSC output (Fig.1B).

There are different types of memory (Morris, 2001) that may be involved in the indirect processing in mammals. None of them require consciousness. Memories can generally be categorized as short-term (or working) and long-term memories (Morris, 2001). A short-term memory may be enough to store RSC inputs through cycles of memory formation and decay (Nairne, 2002). For example, if a male is able to remember a RSC input for 1 hour (although short-term memories are normally considered to be much shorter), he will be able to deliver an RSC output during the first hour following exposure to that specific RSC input. If the male does not encounter any other RSC inputs during that hour, he will forget the initial RSC input and, thus, deliver a non-RSC output (i.e., an output delivered as if in a context not characterized by a high RSC). It must be noted that if a male has not detected any RSC inputs for a considerable amount of time, he may not be anymore in a context characterized by a RSC, and thus a non-RSC output would be an optimal response.

One type of long-term memory involved in the cognitive processing of RSC inputs may be episodic-like memory. Episodic memory is formed in the hippocampus and is involved in the recollection of specific events and the time and space in which they occurred (Baddeley, 2002; Ergorul and Eichenbaum, 2004; Morris, 2001; Squire, 1992). That is, episodic memory allows an individual to remember the "what", "when", and "where" of an event. Although episodic memory assumes consciousness (Baddeley, 2002; Morris, 2001), some animals, for which consciousness cannot be established, show 'episodic-like' memory (Clayton et al., 2003; Eacott and Norman, 2004). Episodic-like memory is also a trial-unique type of memory, that is, only one exposure to the stimulus is required to form the memory (Clayton et al., 2003). This is important for the indirect mode of input processing because in many cases a male may be exposed to a RSC input only once. Episodic-like memory is thus a likely candidate for the indirect mode of input processing, especially if it is advantageous for a male to recall the "what", the "when", and the "where" of RSC inputs. The "what" may be important because different inputs may contain different information in relation to RSC. For example, an old male scent-mark involves less risk of sperm competition than a fresh scent-mark, because in the last case the competitor male is more likely to still be in the area. The "when" may also be important, because the same RSC input contains different RSC information depending on whether the male encountered the RSC input five minutes, five hours or five days ago. The "where" may also be relevant, because a RSC input found near to the location in which a male is going to mate with a given female may represent a higher RSC as compared to the same RSC input detected in a more distant location.

2 Testing the two modes of input processing

When we consider the direct and indirect processing modes separately, there are three general hypotheses about how males may respond to a RSC input. First, males may strictly follow the direct mode of input processing. If so, lesioning specific 'memory areas' (e.g., hippocampus) in the male's brain should not have any effect in how males respond to RSC inputs. Second, males may strictly follow the indirect mode of input processing. If so, lesioning specific 'memory areas' in the male's brain should prevent males from responding to RSC inputs, i.e., both RSC input and absence of a RSC input would result in the same non-RSC output. Third, males may follow both modes of input processing. Males may respond to a RSC input by both reaching a 'RSC state' and forming a memory of the RSC input. Lesioning 'memory areas' in the male's brain should not have any effect in how a male responds to RSC inputs as long as the male maintains his 'RSC state' and is thus 'activated' to respond with an RSC output. However, after the 'RSC state' attenuates or disappears, males with lesioned memory areas should not be able to recollect the RSC input, whereas intact males would be able to recollect the RSC input and deliver an according RSC output, assuming that the memory of the RSC input lasts longer than the 'RSC state'.

The three previous hypotheses are easily testable. For example, males may be assigned to either a CONTROL or a RSC group. In the CONTROL group, males would be exposed to a control or non-RSC input (any stimulus that does not confer a RSC), whereas in the RSC group males would be exposed to a RSC input (e.g., by using odors of conspecific males, delBarco-Trillo and Ferkin, 2004). After a given exposure time, the input should be removed and subsequent measures taken at different times (e.g., at 5, 15, 30 minutes, and 1, 3, 6, 12, and 24 hours) after input removal. For the direct mode of input processing, suitable measurements can include concentrations of plasma hormones, secretion of neurotransmitters, activity or regulation of cellular receptors or enzymes, etc. Many physiological factors may, indeed, play an important role in the processing of a RSC input. For example, some hormones of the hypothalamo-pituitary-gonadal axis (mainly GnRH, LH, testosterone, and estrogen) are key factors in controlling sexual behavior (Hadley, 2000) and, thus, are obvious candidates to be involved in the direct mode of input processing. Other possible factors are oxytocin and dopamine, which have stimulatory effects on sexual motivation, and copulatory and ejaculatory behaviors (Argiolas and Melis, 2004; Coolen et al., 2004; Hull et al., 2004); however, in male rats, exposure to the visual stimulus of another male (a RSC input) does not seem to elicit a dopamine response (Hull et al., 1995). It must be noted that more than one factor may be involved in the direct mode of input processing. For instance, a RSC input may elicit an increase in a given factor, which may promote the delivery of the RSC output by affecting the expression or production of intermediate factors.

The indirect mode of input processing may be tested, for example, by performing selective lesions in specific areas of the brain involved in the formation of memory, such as the hippocampus (Fortin et al., 2004). If lesions in specific areas of the brain impede the expression of an RSC output in males previously exposed to a RSC input, the indirect mode of input processing would be supported. The possibility that lesioning specific brain areas may prevent RSC inputs from even being detected should be obviously controlled. This may be easily done by allowing some lesioned males to deliver their outputs at the same time that they are exposed to the RSC input. When exposure to RSC input and output delivery are simultaneous, no memory formation is required. If such lesioned males deliver an RSC output, this would indicate that their lesions are not affecting the detection of RSC inputs or the normal expression of RSC outputs.

For both modes of input processing, it is important to consider the time that a male is exposed to the RSC input. How much time must exposure to a RSC input last for it to be correctly processed? Are 1 second and 1 hour of exposure to a RSC input functionally equivalent? These questions may be easily tested by exposing different males to the same RSC input for different times (e.g., 5 s, 30 s, 1 min, and 10 min), and then determining whether a longer exposure to the RSC stimulus produces a more intense physiological response or the formation of a longer or different type of memory, and whether this translates in a more intense RSC output.

3 Sperm competition intensity

Sperm competition intensity adds an additional level of complexity to the processing of 'sperm competition' inputs. The 'intensity' of sperm competition (ISC) refers to the number of males competing among them via sperm competition (Engqvist and Reinhold, 2005; Parker et al., 1996; Wedell et al., 2002). Thus, ISC is, as RSC, a continuous variable. When the ejaculates of few males compete for the same set of ova, the ISC is low. Alternatively, ISC is high when the ejaculates of several males compete for the same set of ova. A male may be exposed to varying intensities of sperm competition over his reproductive season, e. g., due to changes in operational sex ratio or population density (Simmons and Kvarnemo, 1997). Therefore, it may be adaptive for males to regulate their outputs (sperm investment or copulatory behavior) in relation to particular ISCs (Parker et al., 1996). Indeed, males generally reduce sperm investment at high ISC compared to low ISC (Pilastro et al., 2002; Schaus and Sakaluk, 2001; Simmons and Kvarnemo, 1997). The reason is that as the number of competing males increases, the benefit of increasing sperm investment decreases (Parker et al., 1996; Wedell et al., 2002).

If males produce different outputs at low and high ISCs (Parker et al., 1996; Pilastro et al., 2002; Simmons and Kvarnemo, 1997), this suggests that males must also perceive and process inputs from the low and high ISCs differently. The main difference between inputs from the low and high ISCs may generally be more quantitative than qualitative. For example, if a male uses odors of conspecific males to assess ISC, odors of only one male will characterize a low ISC, odors of a few males will characterize an intermediate ISC, and odors of several males will characterize a high ISC. The question, then, is how a male may process different quantities of the same type of input (in the previous example, odors of either one, a few, or several competing males) to produce significantly different outputs.

Before answering the previous question we must note that a male may be exposed to several competing males (high ISC) either sequentially or simultaneously. In social and communal breeding species, males will normally be exposed to a high ISC (several competing males) without previously being exposed to the stimuli of only one competitor male (Byrne et al., 2002; McClintock, 1984), i.e., exposure to several competing males will be simultaneous. In most studies that have investigated differences between the outputs of low and high ISCs, males were immediately exposed to inputs of either one or several competitors, respectively (Pilastro et al., 2002). However, in many cases (especially when considering asocial or solitary species), a male may encounter inputs from several competing males sequentially. Hence, it would be interesting to conduct experiments in which treatment males are exposed to three different contexts characterized by inputs of 'one competitor', 'several competitors simultaneously', and 'several competitors in sequence'. Because the 'one competitor' context (or low ISC) is stimulatory (males generally produce the highest sperm investment at low ISC), the initial stimulatory response at low ISC should be inhibited when a male is further exposed to the stimuli of several other males ('several competitors in sequence', a case of high ISC). It must be noted that the factor that is inhibitory at high ISC might be a different factor than the one that is stimulatory at low ISC. That is, instead of one factor that is turned on and off in the low and high ISCs, respectively, there may be stimulatory factors that are turned on in the low ISC and inhibitory factors that are turned on in the high ISC.

We may apply the direct mode of input processing to understand how an inhibitory factor in the high ISC may lower what would have been a relatively high output in the low ISC. Imagine that a male initially encounters the input from only one male (low ISC). This input produces a physiological response involving a stimulatory factor that triggers a 'RSC state' in the male (see Fig.1A). At this point, and as long as the ISC remains low, the male will produce a relatively high output (e.g., high sperm investment). When the male encounters inputs from several other males and, therefore, the context changes from low to high ISC, three different mechanisms may explain why the male may produce a relatively lower output. First, an inhibitory factor triggered in the high ISC may have a direct and negative effect on the output, and this may counteract the stimulatory factor that was activated during the low ISC. Many factors may have negative effects on a male's output (Coolen et al., 2004). Serotonin, for example, may have inhibitory effects on ejaculatory behavior (Coolen et al., 2004). Second, an inhibitory factor may have an effect not directly on the output, but on the stimulatory factor that was acting during the low ISC. As a consequence, that stimulatory factor is turned off or decreased, the male stops being in a

‘RSC state’（or such ‘RSC state’ decreases），and as a result the male produces a relatively lower output. Third，the same stimulatory factor that was acting during the low ISC may be overproduced or overexpressed in the high ISC with negative consequences for the male’s output. That is，there may be a positive correlation between number of competitors detected and production，or expression，of a given factor；however，medium values of that factor may have a stimulatory effect on the males’ output while high values may have an inhibitory effect.

We can also apply the indirect mode of input processing to explain relatively low outputs under conditions of high ISC. When a male encounters the input of only one male（low ISC）he may form a memory of that input（see Fig.1B）. This initial memory may be modified in two ways when the male encounters inputs from several other males（high ISC）. First，the initial memory from the low ISC may be completely substituted by a new memory of the high ISC. This new memory would contain information of the type ‘there are several competitors nearby’ instead of the previous ‘there is only one competitor nearby’. Second，the initial memory may be updated with new information，in the same way that new entries are incorporated into a growing list of data. For example，the initial information ‘competitor 1 nearby’ may be updated to ‘competitor 1 and 2 nearby’ when the male detects a second competitor，subsequently updated to ‘competitor 1，2，and 3 nearby’ when the male detects a third competitor，etc. In both cases，the result is the same；in the low and high ISCs a male forms different memories that，when retrieved，will be translated into different outputs. A memory formed in the low ISC，when retrieved，will produce a high output through stimulatory factors，as discussed above. Alternatively，a memory formed（or updated）in the high ISC，when retrieved，may produce a relatively low output via inhibitory factors or simply by not promoting any stimulatory factors.

4　Conclusion

We believe that our dual approach to explaining the processing of RSC inputs in male mammals is unique and of potential interest to researchers studying sperm competition from different perspectives. Therefore，these modes of input processing should appeal to those researchers that seek to understand male’s adaptations to sperm competition at different levels. Although acknowledging the complexity of the physiological and cognitive mechanisms involved in the processing of RSC inputs，the focus of our approach is to provide a starting point in the study of how males may process such RSC inputs. The lack of research in this area makes the present paper inevitably general and theoretical. We are confident that researchers addressing our hypotheses will fill in the underlying mechanisms that apply to their specific animal models. We also believe that the hypotheses developed in this paper will lead to interesting findings and the development of new and more precise hypotheses.

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