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A Hypothesis About the Biological Basis of Expert Intuition

Philippe Chassy
University of Tübingen

Fernand Gobet
Brunel University

It is well established that intuition plays an important role in experts' decision making and thinking generally. However, the theories that have been developed at the cognitive level have limits in their explanatory power and lack detailed explanation of the underlying biological mechanisms. In this paper, we bridge this gap by proposing that Hebb's (1949) concept of cell assembly is the biological realization of Simon's (1974) concept of chunking. This view provides mechanisms at the biological level that are consistent with both biological and psychological findings. To further address the limits of previous theories, we introduce emotions as a component of intuition by showing how they modulate the perception-memory interaction. The idea that intuition lies at the crossroads between perception, knowledge, and emotional modulation sheds new light on the phenomena of expertise and intuition.

Keywords: chunking, expertise, cell assembly, emotions, intuition

One of the first people to have investigated intuition[1] scientifically is Adriaan De Groot (1946), who studied the psychological mechanisms underpinning expertise in chess. Although De Groot's first intention was to study the problem-solving strategies that enabled world-class players to choose better moves than weaker players, his results indicated that there were no large differences in the way players of different skill levels were carrying out their look-ahead search. For example, the number of positions considered or the depth at which search was carried out did not differentiate much between players of different skill levels. However, a striking result of De Groot's (1946) study was that, within a few seconds, strong grandmasters were able to pick up the key features of the problem situation (e.g., strategic weakness suggesting a possible attack, lack of coordination of pieces making possible a tactical blow). As De Groot (1946) noted, a world champion has as much understanding of the position after looking at it for 5 s as an amateur after deliberating for 15 min. In a separate line of investigation, Polanyi (1964) also noted that skilled perception was an essential component of expertise, a feature he called *connoisseurship*.

Since this early work of De Groot (1946), the phenomenon of intuition has been documented in many domains. A few examples will suffice here. Just as in chess, in several board games strong players can make good decisions surprisingly rapidly. Indeed, in mancala games such as awele, a board game in which players distribute seeds in holes, the rules in some countries prohibit players to think more than 30 s before making a move (Gobet, 2009; Retschitzki, 1990). Physical intuition is often cited as one of the characteristics that differentiate expert from nonexperts in physics. As documented by Larkin, McDermott, Simon, and Simon (1980a), physical intuition enables experts to rapidly construct a complex internal representation of the problem at hand, combining various principles of physics. By contrast, less expert individuals slowly construct a representation centered not on deep physical principles, but on surface characteristics of the problem. Substantial research has been carried out on intuition in nursing (e.g., Benner, 1984; Benner, Tanner, & Chesla, 1992; McCormack, 1993; McCutcheon & Pincombe, 2001; Polge, 1995), a phenomenon that is well documented in this field. Typical examples include nurses picking up subtle differences in newborns' skin appearance as signs of metabolic complications (Klein, 2003), or clinicians immediately recognizing that sweaty and pale appearance together with erratic respiratory and pulse rates suggests a situation critical enough to warrant immediate admission to the resuscitation room (Evans, 2007). Another domain in which intuition plays an important role, both in the popular lore and in the scientific study of expertise, is business. For example, Prietula and Simon (1989) and Klein (2003) documented how executives typically make decisions rapidly and without systematically evaluating the different options available. This result is particularly interesting in that business textbooks recommend a different approach, based on classic economics, in which executives should consider the different options in turn, compute their utility, and choose the option that maximizes their utility. Finally, intuition has been deemed as the method that experts use for making decisions in domains characterized by time pressure, such as fire fighters confronting a blaze or soldiers in a combat situation (Klein, 2003). In these domains and others, an important aspect of expert intuition is that experts choose good options despite the lack of time for making a decision. Klein (2003) went so far to say that experts in these situations do not make a choice, they just apply the first option that comes to their mind.

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Philippe Chassy, Institute of Medical Psychology and Behavioral Neurobiology, University of Tübingen; Fernand Gobet, Centre for the Study of Expertise, Brunel University.

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Correspondence concerning this article should be addressed to Philippe Chassy, Institute of Medical Psychology and Behavioral Neurobiology, Gartenstrasse, 29, Office 309, University of Tübingen, D–72074 Tübingen, Germany. E-mail: Philippe.Chassy@orange.fr

[1] Throughout this article *intuition* refers to *expert intuition*.

Although a number of theories have been proposed to explain how intuition relates to expertise in the domains we have just discussed and in others, no theory has provided a detailed account as to how the proposed psychological mechanisms are implemented neurally. The goal of this article is to fill in this gap, by speculating about the possible neural implementation of the structures and mechanisms proposed by the psychological theory of intuition we have recently proposed (Gobet & Chassy, 2008, 2009). We first review two influential theories of intuition (Dreyfus & Dreyfus, 1988; Simon, 1995) that formed the motivation for our own theory. Then, we discuss in some more detail our theory, which was primarily, but not only, aimed at accounting for intuition in nursing. Finally, we present the biological basis for this theory, both at the neuronal and systems levels.

Theories of Intuition

As reviewed above, there is now strong empirical support for the hypothesis that intuition is a genuine phenomenon. In line with current literature, we proposed elsewhere (Gobet & Chassy, 2008) a list of key criteria for defining intuition: rapid perception and understanding of the situation at hand, lack of awareness of the processes involved, holistic understanding of the problem situation, the fact that experts' decisions are better than novices' even when they are made without analytical means, and concomitant presence of emotional "coloring." This list may be used to evaluate current theories of intuition, which can be classified into two main categories: mechanistic theories (Gobet & Chassy, 2008, 2009; Klein, 2003; Simon, 1995) and nonmechanistic theories (Benner, 1984; De Groot, 1986; Dreyfus & Dreyfus, 1988). We briefly review three of them: Simon's theory (Simon, 1995), Dreyfus and Dreyfus' theory (Dreyfus & Dreyfus, 1988), and our own theory (Gobet & Chassy, 2008, 2009), which is an extension of Simon's theory.

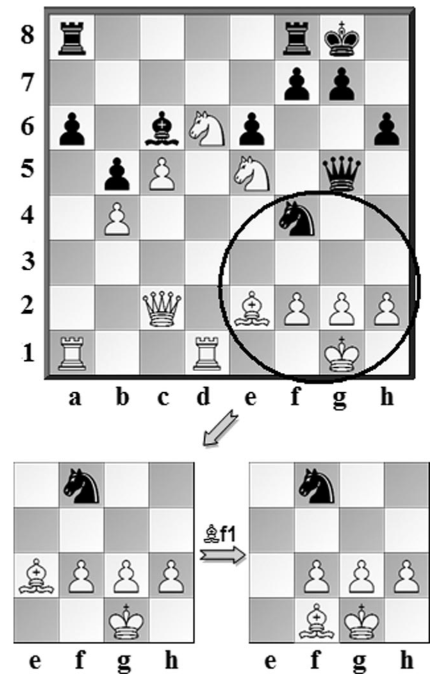

Figure 1. Illustration of how the notion of a production can be implemented using perceptual chunks. A pattern on the board, such as the circled group of pieces on the lower right hand side of the board, may match a perceptual chunk in long-term memory. This will be the condition part of the production. This chunk may suggest possible moves (in this example, the white bishop retreats to the square "f1" to ward off the checkmate threat on "g2"). This will be the action part of the production. Productions are assumed to run unconsciously and intuitively. With expert players and routine problems, productions may lead to actions that are complete solutions to a problem.

Simon's Theory

In a series of publications (e.g., Larkin et al., 1980a; Prietula & Simon, 1989; Simon, 1989; Simon, 1995), Simon developed the idea that, in particular with experts, intuition was mostly due to pattern recognition (see also Bowers, Regehr, Balthazard, & Parker, 1990, for the role of pattern recognition in intuition). During practice and study, experts acquire a large number of perceptual patterns, known as chunks, which encode the key features of the environment. (A *chunk* can be defined as "a collection of elements having strong associations with one another, but weak associations with elements within other chunks"; Gobet et al., 2001, p. 236). For example, in medicine, chunks encode a constellation of symptoms, or in chess, chunks encode the locations of a group of pieces (Chase & Simon, 1973; Gobet & Simon, 1996a, 1998; Saariluoma, 1994). Extensive exposure to a domain also associates information with some of the chunks, such as the kind of action that should be carried out in the presence of a given chunk. What we have here is called a *production* (Newell & Simon, 1972; see Figure 1). Thus, becoming an expert and developing intuitive understanding and acting can be explained by the acquisition of a large number of chunks associated with relevant knowledge. Although nonexperts reach solutions using slow and error-prone problem-solving mechanisms, experts access these solutions automatically by memory lookup. However, despite the fact that they vastly outperform nonexperts in most tasks related to their domain of expertise, experts are hampered by the same cognitive limits as novices (Simon & Chase, 1973). These limits include narrow span of attention and small capacity of short-term memory (STM). In addition, as shown by de Groot (1946/1965), experts essentially use the same problem-solving strategies as novices (e.g., means-end analysis, progressive deepening, and other search heuristics), which are all aimed at cutting down the search space. Simon (Larkin et al., 1980a; Larkin, McDermott, Simon, & Simon, 1980b) implemented his ideas in several computational models, such as a production system simulating the acquisition of expertise in physics.

Dreyfus and Dreyfus's Theory

A rather different explanation was proposed by Dreyfus and Dreyfus (1988, 2005), who rejected mechanistic explanations and instead argued for explanations based on phenomenology. Emphasis was given to the embodied, situated, and experiential nature of human cognition. Given this stance, Dreyfus and Dreyfus's approach is essentially descriptive, and little use is made of experimental evidence.

Dreyfus and Dreyfus (1988) proposed that the road from novice to expert encompassed five stages. During the "novice" stage, individuals acquire information (domain-specific facts, features, rules, and actions) through instruction. At this stage, the rules do not take into account the characteristics of the environment—they are "context free." After considerable concrete experience with the domain, individuals reach the "advanced beginner" stage. The context is now used, and "situational elements"—elements that depend on it—become meaningful. In the next stage, the "competence" stage, behavior becomes increasingly efficient. Decision-making procedures now are characterized by a hierarchical organization, but planning remains essentially conscious and deliberate. Intuition appears only in the "proficiency" stage, in which individuals perceive some features as salient while ignoring others. Although the problem situations are now organized and understood intuitively in this stage, decisions still rely on analytical thinking. Finally, in the last "expertise" stage, not only the understanding of the task but also deciding what to do next is intuitive and fluid. With typical situations, experts do not really solve problems or make decisions, but simply act and carry out the actions that are normally successful. (Gobet & Chassy, 2008, 2009, provided additional details about this theory, described the type of data adduced to support it, and discussed its strengths and weaknesses.)

Although Dreyfus and Dreyfus (1988) criticized standard cognitive explanations of expertise, their own description of the five stages leading from novice to expert shared features with mainstream approaches (cf. Simon's theory above). In particular, the emphasis was on moving from conscious, analytic, and deliberate behavior that depends heavily on instruction to intuitive and fluid behavior that naturally fits the requirements of the environment (Dreyfus & Dreyfus, 1988). An important distinction of Dreyfus and Dreyfus's approach, though, was that it emphasized the holistic nature of experts' cognitive processing. Dreyfus and Dreyfus also speculated that connectionist models of associative memory (Hinton & Anderson, 1989) could emulate the holistic nature of intuition, and that aspects of experts' learning could be explained by the approach of reinforcement learning (e.g., Tesauro, 1992).

With respect to the criteria that we highlighted above, Simon's theory fares well with rapid perception and understanding, lack of awareness, and the fact that experts' decisions are better than novices. Dreyfus and Dreyfus also emphasized these features, but did not provide detailed mechanisms for them. By contrast, they did emphasize the holistic nature of intuition, which was explicitly criticized by Simon and Barenfeld (1969). Both theories have little to say about how emotions link to intuition.

Template Theory of Intuition

To provide a more thorough coverage of the phenomena linked to intuition, we have recently extended the template theory of expertise (Gobet & Simon, 1996b, 2000) to the realm of intuition (Gobet & Chassy, 2008, 2009). In a sense, the new theory takes the best from the two theories that we just presented. From Simon's (1995) theory, it borrows the ideas of chunking, pattern recognition leading to potentially useful actions, and the notion that experts share with novices the same cognitive limitations (e.g., limited short-term memory, limited span of attention, and slow learning rates). From Dreyfus and Dreyfus's (1988) approach, it borrows the idea that intuition enables a holistic grasp of the situation.

The key addition in template theory is the idea that chunks that are used often in experts' practice develop into more complex memory structures, known as templates, which are analogous to what is known as "schemata" in the psychology literature (Bartlett, 1932; Broadbent, Cooper, & Broadbent, 1978). Templates, which are a special type of chunk, possess both a core, made of stable information, and slots, made of variable information. For example, in the schema of a "room," the fact that rooms have a floor, a ceiling, and walls, would constitute the core, whereas the number of doors and windows would be encoded as variables. (Another example of a template, in the context of chess, is presented below.) A criticism of earlier schema theories, including theories of knowledge representation and semantic representation in classical artificial intelligence (AI), was that they were rather vague as to how schemata are learned. This criticism does not apply to template theory. Detailed mechanisms are specified as to how the information held in templates—both in their core and their slots—is acquired incrementally. In addition, the theory provides mechanisms about how new values can be rapidly stored in the slots (in about 250 ms; Gobet & Simon, 2000).[2] Not only do templates enable a rapid storage of new information into long-term memory (LTM), but they also make it possible to "glue" together smaller chunks. Thus, one weakness of Simon's (1995) earlier account—the relative small size of the chunks he hypothesized—is removed in the new theory.

Computational Instantiation of the Template Theory: The CHREST Model

A strong support for this new theory of intuition comes from the fact that several aspects of the original template theory have been implemented in a computational model, CHREST (chunk hierarchy and retrieval structures). CHREST is a computer program originally developed for simulating several phenomena in chess perception and memory, such as the detail of the eye movements carried out, the type of errors made, and the kind of groupings used in a memory task (De Groot & Gobet, 1996; Gobet & Simon, 1996b, 2000; Gobet & Waters, 2003). In recent years, the scope of CHREST has broadened, and simulations have now been carried out, well beyond chess, in domains including problem solving in physics, memory for computer programs, concept formation, verbal learning, vocabulary acquisition, and syntax acquisition (e.g., Freudenthal, Pine, & Gobet, 2009; Gobet & Lane, 2010; Gobet et al., 2001; Jones, Gobet, & Pine, 2008).[3] Given its purpose and use, CHREST should not be seen as an AI program, but rather as a computational architecture of human cognition. In the following, we use chess to illustrate the components and mechanisms of CHREST, first because chess offers some the best empirical evidence for intuition, and second because both Dreyfus and Dreyfus and Simon often used chess in their analysis of intuition.

[2] We refer readers to Gobet and Simon (2000) and Gobet and Chassy (2009) for a detailed description of these mechanisms.

[3] The code of CHREST, written in Common Lisp and Java, can be obtained at www.chrest.info.

With CHREST, chunks and templates are accessed through a discrimination network (Simon & Gilmartin, 1973), which is a network of tests that enable access to nodes that store LTM information; these nodes can be either chunks or templates. Learning is slow (e.g., it takes 10 s to acquire a new chunk), but once a chunk has been learned, access is fast (a few hundred milliseconds). Thus, objects are assumed to be recognized rapidly, as it is indeed the case with humans.

Apart from the discrimination net, the model has three components: an LTM, a visual STM, and a "mind's eye." LTM holds chunks, templates, and productions. Visual STM has a limited capacity (three chunks). If a new chunk enters STM when it already contains three items, the oldest chunk is discarded and replaced by the new one. The exception to this is that the largest chunk stays in STM unless a larger chunk has been recognized. The mind's eye maintains visuospatial information for a limited amount of time (less than 1 s if the information is not refreshed). It is also the place where visuospatial information is manipulated—for example, in chess, the trajectories of pieces are computed there. With respect to mechanisms, CHREST primarily uses four sets of them: STM management, LTM learning, management of eye fixations, and information update in the mind's eye. A central assumption of CHREST is that humans have conscious access to the information held in STM and in the mind's eye, but that all other information and all processes—including those used during learning and recognition—are not accessible to consciousness.

The model simulates eye movements using a combination of simple heuristics and the information held in LTM. After each fixation, the information in the field of view is sent to the discrimination net. With chess, the field of view includes the square being fixated plus or minus two squares in each direction, assumed to be perceived in peripheral vision; thus at most 25 squares can be perceived together at any time (see De Groot & Gobet, 1996, for the reasons behind this choice).

CHREST uses two learning mechanisms for the creation and expansion of chunks: discrimination and familiarization. When an object is perceived, the features extracted from it are sorted through the discrimination net. After a node has been reached, the object is compared with the information held by this node (this information is called the *image*). There are two possible cases. First, if the image contains less information than the object,[4] new features are added to the image; this process is called *familiarization*. Second, if there is a mismatch between the object and the information in the image, a new node is created below the current node. The process is called *discrimination*. CHREST also creates similarity links between nodes. When a chunk arrives into STM, its image is compared with that of the largest chunk already stored in STM. When chunks share enough elements, a similarity link is created between them. During recognition, similarity links can be used to switch from one node to other similar nodes.

Templates are chunks augmented by at least one slot in which variable information can be stored. Figure 2 presents an example of a chess template acquired by CHREST. The pieces on the board constitute the core of the template. The two dots (on the squares d2 and g2) indicate the presence of slots for these squares; that is, these square slots might contain a piece, whose identify will be encoded (variable instantiation) when a specific board is seen. The icons below the board for black pawn and white bishop, knight and pawn indicate the presence of slots for pieces. These piece slots can encode different locations on the board, depending on the board currently being perceived.

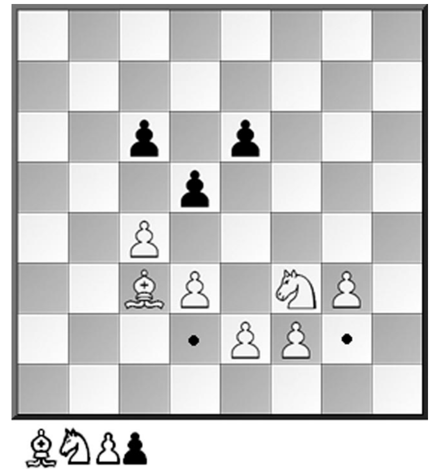

Figure 2. Example of a template acquired by CHREST (chunk hierarchy and retrieval structures). The pieces on the board indicate the core of the template; the dots on squares indicate square slots where pieces can be encoded, and the piece icons below the board indicates piece slots where squares can be encoded.

Slots are created when two conditions are met. First, the target node must be sufficiently large. Second, enough nodes below the target node must share related information.[5] The mechanism for slot creation is illustrated in Figure 3. The node depicted in gray has four children; the information "white pawn" occurs thrice, and the information "square e4" occurs twice. Assuming that the minimum number of occurrences is two and the target node is large enough, slots would be created as indicated in the figure.

All cognitive operations carried out by the program have a time cost, which makes it possible to simulate in detail the time course of human behavior, including the first hundreds of milliseconds critical for an understanding of intuition. During the learning phase, CHREST incrementally acquires chunks and templates by moving its simulated eye around representative situations (e.g., in the case of chess, positions taken from master games). It also automatically associates potential actions (in the case of chess,

[4] Information is measured as the number of primitives held in a chunk (i.e., the image of a node). In chess, primitives are pieces on a given square (e.g., white queen on square h4). It is obvious that primitives vary from domain to domain. For example, in the simulation of the acquisition of vocabulary, primitives are phonemes; and in the simulation of the use of diagrams in physics, primitives are graphical elements such as lines. We also note that the list-structure coding used by CHREST for the input offers a more flexible data type than the fixed-size arrays usually used by connectionist models. As can be seen by the number of domains in which simulations have been carried out by CHREST, its learning mechanisms are very general.

[5] In the chess simulations, the requirement is that the target node contains at least five elements and that at least three nodes below that node share identical information (either a square, a type of piece, or a chunk; see Gobet & Simon, 2000).

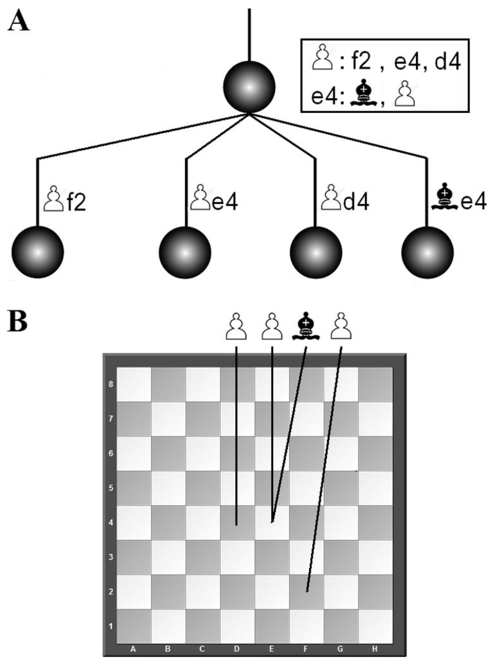

Figure 3. The mechanism of template formation. Panel a shows the portion of a discrimination net, and Panel b shows the piece locations on the chessboard. A slot can be created when, under a given node in the discrimination network, some information of the same kind recurs often. The slot added to the target node specifies both the variable and the values that this variable can have. In the figure, a slot can be created for "white pawn" because a white pawn appears in three branches below the node depicted in gray. The possible values for the squares containing the pawn are "f2," "e4," and "d4." Similarly, a slot can be generated for the square "e4," which has the values "black bishop" and "white pawn." Thus, templates are simply chunks with slots.

moves) to perceptual patterns (see Figure 1). All learning—acquisition of chunks, creation of templates, acquisition of possible actions and their possible connection to chunks—is done automatically using naturalistic input material that is representative of the structure of the environment met by (human) experts. That the system learns in an unsupervised fashion and that the network is self-organizing are also features that are of interest for explaining expertise and intuition. Another important aspect of the model is the tight link between perception, learning, and attention. In particular, information linked to chunks may guide eye movements and attention in similar situations, which is in line with the importance of perception in intuition.

Simulations with CHREST have established that it accounts for a wide range of data on chess perception, mental imagery, and memory for players ranging from weak amateurs to grandmasters. For example, the model can simulate eye movements during the 5-s presentation of a position; the recall performance in memory experiments with game positions as well as with positions randomized in various ways; the effect of presentation time on recall (from 1 s to 60 s); and how novices acquire chunks and templates (De Groot & Gobet, 1996; Gobet & Clarkson, 2004; Gobet & Simon, 2000; Gobet & Waters, 2003; Waters & Gobet, 2008).

The Link Between Emotions and Cognition

An important feature of the new theory, which was neglected by the other two theories, is the provision of mechanisms linking emotions and intuition. Emotions are short-term, object-specific changes that tune body and mind to respond quickly and efficiently. Each emotion leads to a specific pattern of activity in the autonomic nervous system (Collet, Vernet-Maury, Delhomme, & Dittmar, 1997), a process whereby it prepares the body to perform appropriate actions (see Frijda, 1993, for the concept of action readiness). By modulating how information is processed in many cognitive components, emotions fine-tune the cognitive system (Russell, 2003) to adapt to current goals. For example, if someone unfortunately meets a bear in a forest, fear will have two crucial effects: (a) prepare the body to flee (e.g., increase in heart rate) and (b) focusing attentional resources on the dangerous animal.

Critical to our argument of incorporating emotions in a model of intuition is the influence of emotions on the two crucial processes involved in intuition: perception (Charash & McKay, 2002; Eastwood, Smilek, & Merikle, 2001; Lerner & Keltner, 2001; Öhman, Flykt, & Esteves, 2001) and memory (Erk et al., 2003; Kensinger & Corkin, 2003; Lewis, Critchley, Smith, & Dolan, 2005). Of particular interest are basic emotions (Ekman, 1999; Izard, 1992; Oatley & Johnson-Laird, 1987; Orthony & Clore, 1989), an inherited repertoire of automatic responses shared by all members of a given species. Basic emotions are recognized early in the development of infants (Serrano, Iglesias, & Loeches, 1992). It is on this emotional-cognitive system that infants develop more sophisticated emotions.

Ontologically constructed emotions differentiate from the basic ones along with experience (Izard & Malatesta, 1987; Plutchik, 1980; Sroufe, 1979). They might include a cognitive component that makes them more prone to individual variability (Lewis, 2008). For example, ontological emotions are felt differently in different cultures (Eid & Diener, 2001). Yet, this difference does not hamper their influence on cognitive processes (Abe, 2004). The relevance of emotions in a theory of intuition is thus grounded in the fact that emotions have a marked influence on cognitive processes at all levels.

There is now strong empirical evidence that representations used in decision making are associated with emotional values. A particularly strong example is provided by Bechara, Tranel, Damasio, and Damasio (1996), and it is worth presenting this study in some detail. Their experiment used a decision-making task involving the use of economic values. Four packs of cards were presented. Within each pack, each card could win or lose money. However, each pack was designed so that it would either win or lose money on average. At the start of the experiment, participants were awarded a fictional bank account with $2,000. They could pick one card at a time from any pack. While participants were continuously making decisions as to which card to choose, skin conductance was recorded. The results revealed that, after some trials, healthy participants tried to avoid the two packs leading to loss of money. Patients with prefrontal lesions, on the other hand, did not avoid the losing packs. Crucially, whereas the healthy participants showed differences in skin conductance when they were about to take a card from a positive compared to a negative pack, the participants with brain lesions did not show any differences.

This result has shed a new light on how emotions infiltrate high-level cognition. It has long been believed that deliberate thinking played a central role in decision making, and it does indeed play such a role in understanding the problem situation. However emotions, although neglected for a long time, also play a critical role. To be specific, in Bechara et al.'s (1996) experiment, emotions start playing their part after an individual has selected a pack. The feedback from the environment (i.e., gain or loss of money) causes the pack to be tagged by an emotional response. Hence, the next time an individual plans to engage in the same course of action that has been previously harmful, negative emotions will send a signal preventing her from proceeding. When the action is not associated with an emotional response, the individual is blind to past experiences. Bechara et al.'s experiment clearly showed that emotions are necessary to carry out everyday decision making or problem solving. It also illustrated that emotional responses reflect the perceived benefit or harm of the situation. As noted in the early literature on expertise (De Groot, 1946/1965; Tikhomirov & Vinogradov, 1970), emotions are also important in the development and maintenance of intuition.

The mechanism we propose for linking emotions to intuition is simple, but also well supported by the empirical evidence we just reviewed. While studying a domain of expertise, one learns not only perceptual chunks, as noted above, but also which elements are useful, detrimental, or neutral to a task. This is made possible by chunks getting associated with reward or punishment. When memory structures get fused through chunking, their emotional relevance is also recomputed to reflect the utility of the newly stored item. In the future, emotional responses will help draw attention to the chunks that are most useful in the problem situation and thus orient the individual toward some solutions rather than others.

Evaluation of the Theory at the Psychological Level

Our theory fares well with respect to the five criteria we identified in the introduction as signatures of intuition, not the least because it combines the best features of Simon's (1995) and Dreyfus and Dreyfus' (1988) theories. From the former theory, it inherits mechanisms for the rapid perception and understanding of the situation, as well for the lack of consciousness of the processes engaged and the fact that, with experts, intuitive decisions tend to be correct. From the latter theory, it inherits the notion that understanding of the problem situation is holistic (through the use of templates). Finally, unlike the two earlier theories, it provides processes explaining how intuitions are colored by emotions.

Despite these positive features, one important limit of the new theory (shared by other theories of intuition) is that it did not provide an explanation of how the mechanisms it postulates are implemented biologically. In the remainder of this article, we provide such an implementation, focusing on the chunking mechanism.

A Biological Implementation

Our discussion is divided into three main sections. First, we discuss mechanisms at a fairly low level, that of cell assemblies. Second, we deal with the systems level, and show how the development of expertise and intuition affects the way with which information is processed in the brain from early posterior visual areas to more anterior perceptual and memory areas. Finally, we take up the question of emotions, this time discussing it from a neural point of view.

The Concept of Cell Assembly

Because the neuron has been established as the unit of the nervous system by the Spanish anatomist Ramón y Cajal (Cajal, 1889, 1906) at the turn of the 20th century, scientists have tried to unravel how neural activity underlies psychological activity. For a few, well-documented cases, such as sensitization and habituation, the link between neural activity and behavioral changes has now been empirically established (Kandel, 2001). However, cases in which this has been done constitute the exception rather than the rule. For many high-level, complex forms of cognition, the attempts to associate neural activity with cognition are circumscribed to theoretical proposals (Dehaene, Cohen, Sigman, & Vinckier, 2005; Eggermont, 2001).

For decades, a central research question has been to understand how objects are coded in neural networks. Recently, neuroimaging techniques have yielded useful information about this issue. The first key finding is that neural networks coding visuospatial objects are distributed in several visual modules, thus involving a great number of neurons (Levy, Hasson, & Malach, 2004). Even though data have shown that specific neurons respond preferentially to specific categories of objects (Booth & Rolls, 1998; Kanwisher, McDermott, & Chun, 1997), they can do so only because discrimination has been carried out before. Neuroimaging experiments have shown that object recognition takes place in the inferotemporal cortex, a cortex where representations are stored (Aggelopoulos, Franco, & Rolls, 2005; Desimone, 1991; Haxby et al., 2001; Miyashita, Date, & Okuno, 1993; Sigala, 2004; Spiridon & Kanwisher, 2002). We find it interesting that synchronized neural activity at gamma band ($F > 30$ Hz) correlates with perceptual processing (Tallon-Baudry, 2003; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). Unity of a percept and efficiency of processing depend on the efficiency with which synchrony firing takes place (Castelo-Branco, Goebel, Neuenschwander, & Singer, 2000; Glassman, 1999; Mima, Oluwatimilehin, Hiraoka, & Hallett, 2001; Tallon-Baudry, 2003). When neurons fail to fire in synchrony within this specific frequency band, perception is impaired (Spencer et al., 2004). Gamma band synchronization offers an example of how neural units combine to form a dynamical entity, which, remarkably, is reflected at the behavioral level by the emergence of a percept. Gamma band synchronization is a neural indicator of the mechanisms underlying cognitive operations—here feature binding—and thus bridges the gap between cell and behavioral levels, allowing in this way to build theories in psychology that are biologically testable.

Strikingly enough, all these properties fit into the theoretical concept of *cell assembly* introduced in the 1940s by Hebb (1949). Cell assemblies are formal, theoretical entities able to recruit neurons in several brain modules. This concept has turned out to be an astonishing insight. Since Hebb's book in 1949 and in particular in recent years, various researchers have theorized on the properties of cell assemblies (e.g., Braitenberg, 1978; Palm, 1982; Pulvermüller & Mohr, 1996; Sakurai, 1998; Singer et al., 1997;

Wennekers, Sommer, & Aertsen, 2003; Wickelgren, 1992). A cell assembly is a group of interconnected neurons that network to form a biologically and psychologically functional unit. The functional unity is ensured at the neural level by synchrony firing. Should synchrony firing be prevented, for example as a consequence of a disease (e.g., Grice et al., 2001), the psychological unit (i.e., the percept) would not be operative. Cell assemblies can be considered as complex entities insofar as they involve a large, densely interconnected number of units that might display complex dynamical patterns (Elbert et al., 1994). For example, in the real brain, more than a million neurons are involved in the recognition of a single object (Levy et al., 2004). Also, the mere fact that each neuron makes connection with approximately 1,000 of its peers (Churchland & Sejnowski, 1992) provides a first clue about the high level of complexity and density that is necessary for a cell assembly to be operative. These low-level properties are the foundations on which researchers have further developed the concept recently.

After close examination of the structural characteristics of a cell assembly, Sakurai (1998) listed its main dynamical features. First, a cell assembly is a dynamic construction; it is a temporally active set of neurons. Second, it has a dynamic persistence; activation of a cell assembly will persist via reentrant loops. The third characteristic is dynamic completion; in the presence of strong connections, activation of a large enough subset results in the activation of the entire cell assembly. Finally, as noted above, the characteristic of high distributivity is important; a cell assembly can activate neurons distributed in different brain areas (Bushara et al., 2003). A corollary of these characteristics is that neurons code the properties of an object and not the whole object. For example, the property "white" of a white bishop is coded by a set of neurons, each typically responsive to one of the aspects constituting the exact nuance of white of this object. The same set of neurons will be activated not only by the other white pieces but also by objects (e.g., a fridge) that have this nuance of white. The point is that the set of "white color" neurons will be associated with other sets coding for other properties to form a large cell assembly. The other sets of neurons encoding different visual features will differ, for example, between the fridge and the bishop; hence, even though both objects use the "white neurons" assembly, their coding will differ. As the property coded for by a set of neurons is shared by different objects, the set of neurons can be involved in the coding of several objects.

Cell Assemblies, Chunks, and Intuition

According to chunking and template theories, a huge part of experts' performance is due to LTM structures. Here, we use the fact that learning these memory structures occurs through neural plasticity to provide a key insight into the mechanism that underlies intuition. Two facts have to be borne in mind to understand this mechanism. First, the activity of any neuron propagates to some extent to all the neurons it is connected with. Second, plasticity occurs when connected neurons are simultaneously active.

Figure 4 is a diagrammatic representation of the information processing taking place during object recognition. The up arrows show the direction of the neural signal while it is processed bottom up. For sake of clarity, neurons belonging to the same neural assembly have been grouped together and shown as gray circles. Let us detail how the processing of visual information progresses until recognition is completed. The signal starts from the receptors of the retina, where photonic energy is transduced into neural information. The signal is then forwarded via the lateral geniculate nucleus to low-level visual areas, from where it follows the so-called ventral pathway (Ungerleider & Mishkin, 1982). The route ends in the inferior temporal (IT) cortex where recognition takes place by synchronous activation of a cell assembly coding for the perceived object. From there, the activity of the cell assembly diffuses and activates object-related knowledge in other brain modules (e.g., spatial or semantic modules). The neurons that are the key to our discussion are located in the IT cortex. The activity of IT neurons is necessary for recognition to take place, as some of these neurons are the biological substratum that embodies visual memories (Booth & Rolls, 1998; Kanwisher et al., 1997; Kawasaki et al., 2001; Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). Chunks are representations of visuospatial objects that are "glued" together so that they form a new, single visuospatial unit. Within the framework of Figure 4, chunking is conceived as the horizontal association of cell assemblies. If two objects are coded by two

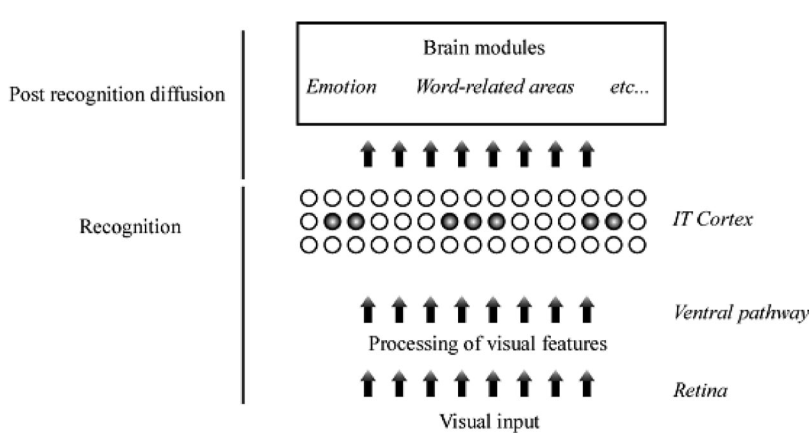

Figure 4. The stages leading to pattern recognition and postrecognition diffusion. The gray circles indicate cell assemblies in IT (inferior temporal) cortex.

different cell assemblies, then their chunking leads to the coding of a new object that mixes visual features of the two chunked objects. The visual object that is recognized can be more complex and encompass much more visual information.

Figure 4 thus offers a clear illustration of how chunking occurs at the neural level. A striking feature to be borne in mind is that the number of recognizable objects as well as their visual complexity only marginally impact on the number of steps necessary for processing visual features to complete recognition, assuming that these objects have been chunked. This implies that the parallel character of the system enables improvement in performance without loss in time. A visual object (e.g., a configuration of chess pieces) is associated with properties and functionally related information that may be encoded in the same visual area (e.g., a related piece configuration) or different brain areas (e.g., a strategy). The activity of cell assemblies in the IT cortex propagates to areas in which object-related information is coded. The mental construction of the situation problem terminates (before the next cycle of refreshment) once the propagation of the neural signal has eventually activated object-related material.

Intuition, a different process from chunking, shares some properties with it. We have seen that one property of intuition is the immediate understanding of the problem situation at hand. Referring to Figure 4, intuition corresponds first to the pattern of cell assemblies activated as a result of recognition, and second to the diffusion of the neural signal from these active cell assemblies to object-related areas (i.e., postrecognition diffusion in Figure 4). A densely connected network offers a better diffusion of activity so that more relevant items may come into consideration, thus raising the probability of finding the correct solution.

Let us detail the processes underpinning the development of intuition. For sake of clarity, we simplify and decompose the process in two phases. The first phase is essentially of perceptual nature: Perceived objects activate a corresponding number of cell assemblies (for details, see Freiwald, Kreiter, & Singer, 2001). The basic principle is that neurons belonging to a cell assembly fire in synchrony. The first evidence of synchrony firing at the neural level has been provided by C. M. Gray and Singer (1987) when analyzing the neural dynamics of cats' visual cortex (C. M. Gray, König, Engel, & Singer, 1989). Large populations of neurons firing in synchrony produce a detectable response: a so-called oscillation (Buzsaki, 2006). Oscillations are characterized by their frequency and interpreted with respect to the anatomical location in which they occur. A crucial oscillation regarding the formation of cell assemblies is the gamma frequency band (Fries, Nikolic, & Singer, 2007). C. M. Gray and Singer's findings regarding oscillatory activity have been extended to humans by studies monitoring the activity in the gamma frequency band (Rodriguez et al., 1999; Tallon-Baudry, 2003; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996; Tallon-Baudry et al., 1998). In bistable percepts, such as the Rubin illusion, switching perceptual organization from one object to another modulates gamma band activity in neurons (Basar-Eroglu, Strüber, Kruse, Basar, & Stadler, 1996). Finally, it is established that when oscillatory activity cannot take place, perception does not occur (Uhhaas & Singer, 2010). These empirical findings confirm numerous aspects of the theoretical research and simulation results on binding (see the review by von der Malsburg, 1999). As a consequence of these perceptual processes, we can posit that numerous neurons coding for object properties oscillate in synchrony. Thus, learners first perceive the items that will be the object of learning.

The second phase concerns learning, in which the properties of the items are associated with potential solutions. Simultaneous firing acts as a trigger for synaptic plasticity (Cruikshank & Weinberger, 1996; Okatan & Grossberg, 2000; Wespatat, Tennigkeit, & Singer, 2004). Neural plasticity, which has been the focus of numerous studies in neurobiology, is the biological process by which a neuron adjusts its influence on a target neuron. Long-term synaptic plasticity is the biological phenomenon underpinning skill acquisition (Luft, Buitrago, Ringer, Dichgans, & Schulz, 2004) and long-term, declarative memory formation (Cooke & Bliss, 2006). The process is synapse-specific (Martin et al., 1997), so that neurons can reorganize the dynamics of a network with a high degree of precision. The molecular cascade of events leading to synapse formation is well characterized (see Kandel, 2001, for a detailed review), thus offering an example of how molecular events affect behavioral performance. While learning progresses, neural connections are rewired to capture the essence of problem situations of increasing complexity so that intuition becomes more reliable. The binding of items with other items and the increasing number (and complexity) of procedures and potential solutions in memory are at the core of expertise acquisition (e.g., for chess, Chase & Simon, 1973; Gobet & Simon, 1998; music, Glassman, 1999; computer programming, Vessy, 1987).

As Figure 4 displays only three chunks, the processes of recognition and postrecognition diffusion may seem trivial; however, it should be borne in mind that prior research (Gobet et al., 2001; Gobet & Simon, 2000) has demonstrated that, at least in some domains, top experts have learned around 300,000 chunks. The sheer magnitude of this number makes it easier to understand that the development of intuition, through chunk learning, can lead to a dramatic increase in performance. Here also, the strength lies in the parallel nature of the processing. First, all the chunks (i.e., around 300,000) are in competition for perceptual dominance; recognition takes only a few steps whatever the visuospatial complexity of the situation problem. Second, recognized chunks propagate their activity to relevant information that was associated with them.

The Biological Link Between Emotions and Intuitions

When describing the template theory of intuition, we proposed a mechanism whereby an emotion is associated to a stimulus. Biologically, this mechanism is a rather natural extension of Hebbian learning: The organism uses neural plasticity not only to fuse cognitive items together but also to pair an item with an emotional response. The conditioning fear paradigm has provided a perfect example of how a neutral sound comes to be paired with the fear response. LeDoux (1999) details how the pairing takes place by Hebbian plasticity in the amygdala. Emotional responses have a unique neural signature as reflected by the pattern of activity of the neural networks in charge of processing emotional information (Damasio et al., 2000). In his 2004 article, Rolls provided a theoretical account of how emotions coded in the prefrontal cortex were paired with percepts of various modalities. In doing so, he showed that the neural emotional signature might be paired with a cognitive item. In the case of fear conditioning, the relationship between the emotional and the cognitive systems is unidirectional:

An item triggers an automatic emotional response (LeDoux, 1999). To a simple problem (e.g., a danger), the mind has a single and simple response, preparing the body for fleeing (i.e., fear). This simple system may not be adequate to account for the influence of emotions on cognitive functions belonging to a higher level, such as intuition in problem solving. This is a crucial difference between mere reinforcement of a behavior and our view of the contribution of emotions.

Problem solving, in particular when involved with abstract concepts, may require the combination of various items and thus the integration of a few, and possibly different, emotional responses. Emotional systems (e.g., in charge of joy, fear, and disgust) assess the emotional value of various items in parallel. Typically, emotional assessments are integrated to form a global emotional response (Park et al., 2010). At the end, the emotional response is supposed to influence the cognitive system selectively (J. R. Gray, Braver, & Raichle, 2002). Yet, multithread emotional processing leads, in some circumstances, to the generation of inconsistent emotional responses (Wittfoth et al., 2010), which might confuse the cognitive system. The emotional system resolves the conflict before cognitive processes move on to the next stage (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006). This emotional integration of emotions is a crucial aspect of intuition because the emotional response will orient further cognitive processing. Such an emotional conflict resolution obviously entails emotional computations that are not found in simple forms of emotional learning. With respect to complex tasks, and even though it is felt as quick, emotional conflict resolution requires the integration of many emotional responses. This integration is a crucial aspect of intuition in that it can orient cognition toward one solution rather than another, and this process takes place outside conscious control. In addition to this, the propagation of the activity generated by the recognized items to other items in the expert's web of knowledge might generate yet other emotional responses, as evidence by the mood congruity effect (Bower, 1981; Mayer, Gaschke, Braverman, & Evans, 1992). How, then, is the cognitive system able to compute a quick, but nevertheless accurate, solution to the problem at hand?

Our answer is that intuition is the result of a triangular interaction between pattern recognition, procedural knowledge, and emotional modulation. Figure 5 illustrates how this triangulation works.

Figure 5 is made of three panels. Panel A shows that the recognition of domain-specific patterns (each displayed with a different visual appearance in the figure) activates potential solutions (e.g., a typical tactical maneuver in chess) and elicits emotional responses. It is worth noting at this point that various emotional responses are actually coded in different brain structures and that the block of neurons displayed in the figure is clustered to facilitate understanding. Similarly, procedural knowledge can be encoded in many brain structures and has been clustered in the figure. Panel B shows that, following the integration of various emotional responses, the global emotional response modulates both pattern recognition and the levels of activity in memory.

As emotional and cognitive processes are running partly in parallel, we have summarized both "pipelines" in Panel C. The first step for both pipelines is when the problem solver recognizes a series of patterns (coded as three assemblies of neurons) that in turn activate or inhibit several components of the emotional system (represented in Figure 5 as three assemblies of neurons). The emotional system integrates the inputs, resolving potential conflicts, and generates an overall response that is diffused in the cognitive system (Figure 5, Panel B). The diffusion of the emotional information modulates the level of activity of congruent and incongruent cognitions so that the emotional information biases the selection of possible solutions. Finally, another well-documented aspect of emotions is their influence on attentional processes (see Taylor & Fragopanagos, 2005, for a review). In visual scenes requiring more than one eye fixation (such as chess problems), emotions influence bottom-up processing of entrant stimuli. The emotional saliency map may interact with the attentional saliency map to select which information will be picked up from the environment. Despite all these interactions between components, we can still talk about a triangular relationship, as attentional processes can be seen as an aspect of pattern recognition.

Intuition emerges from the process of integrating perceptual blocks together with relevant knowledge and emotional modulations. The triangular structure of intuition is possibly the reason that made this psychological phenomenon so difficult to explain. Skill acquisition and expertise have often been studied using behavioral evidence with few or no reference to biological models. In addition, emotions have been until recently a relatively minor topic in psychology. As a consequence, the understanding and modeling of emotional events was lagging behind the modeling of cognitive phenomena. Finally, the concept of a cell assembly has been applied to well-targeted cognitive phenomena belonging to perceptual (Fell, Fernández, Klaver, Elger, & Fries, 2004; Knyazeva, Fornari, Meuli, Innocenti, & Maeder, 2006; Laurent, 1996; Meador, Ray, Echauz, Loring, & Vachtsevanos, 2002), memory (Axmacher, Mormann, Fernández, Elger, & Fell, 2006; Eggert, Bauml, & van Hemmen, 2001), and motor processes (Wickens, Hyland, & Anson, 1994). Many studies on cell assemblies have analyzed how they behave in various circumstances or have attempted to improve their explanatory power (Freeman, 1983; Vico & Jerez, 2003). In addition, the exact definition of neural assemblies has changed from one paper to another, which does not allow bridging the gap between domains. Because these strands of research were unable to communicate together or showed poor cooperation, formalisms accounting for intuition were limited in theoretical depth. Our theoretical framework strengthens and extends the cognitive view originally put forward by Simon (1995) and adds the emotional and biological aspects to the whole theoretical picture. Our view integrates a vast amount of data from psychology, biology, and cognitive science. Finally, as the time course of the main events is spelled out and the mechanisms generating intuition specified, we provide a ground for future empirical research.

The triangular theoretical framework presented here is well supported by empirical data. Neuroimaging evidence has convincingly shown that object recognition takes place within the ventral visual stream (Haxby et al., 2001; Haxby, Hoffman, & Gobbini, 2000; Kanwisher et al., 1997; Liu et al., 2008; Mei et al., 2010; Vinckier et al., 2007). The link between object recognition and automatic emotional responses is well documented (Rolls, 2004; Vanderploeg, Brown, & Marsh, 1987). Hence, object coded as cell assemblies along the ventral visual stream are associated to cell assemblies located in other areas. The link between emotion and attention also has been the focus of much research (Eastwood et al.,

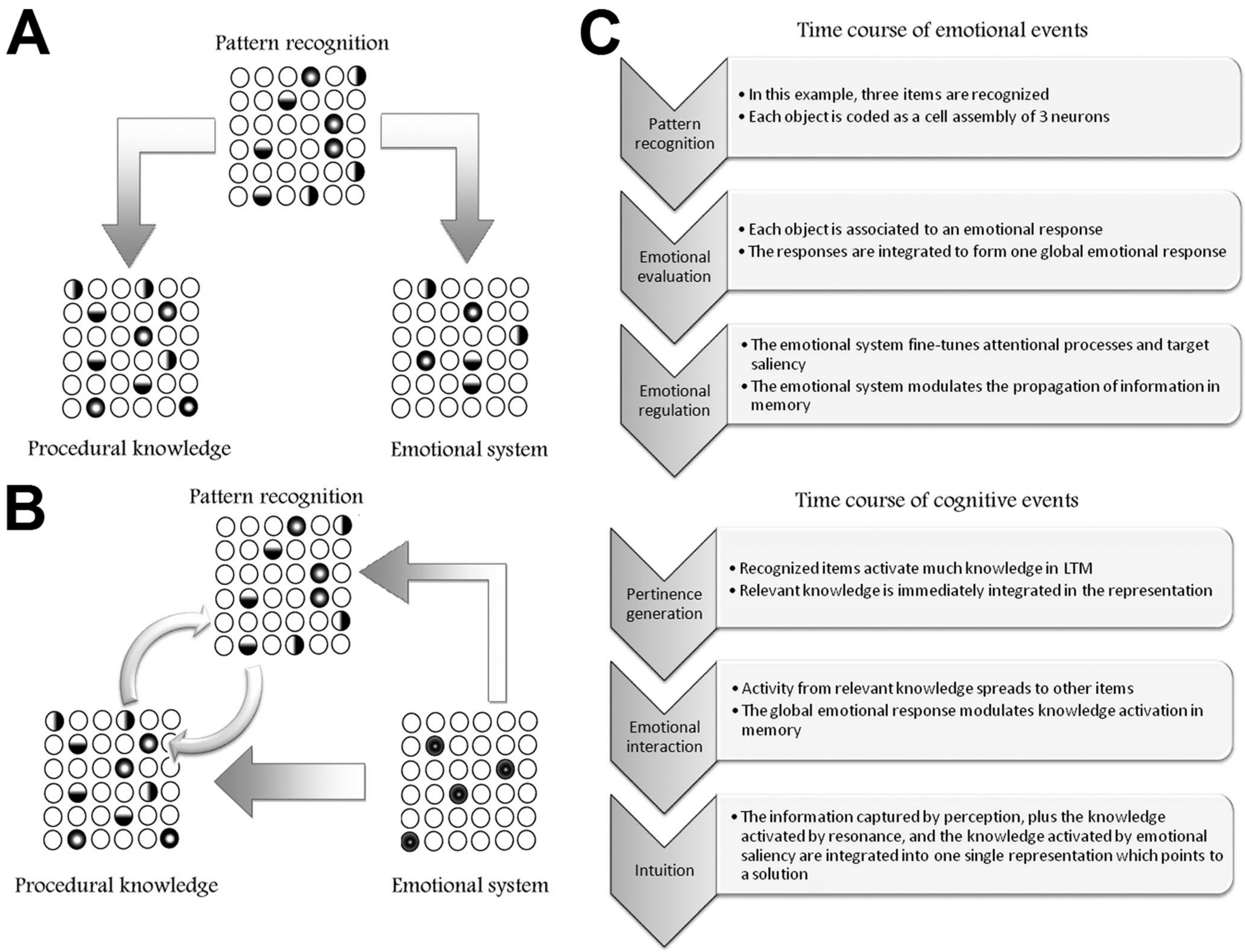

Figure 5. The triangular relationship between patterns, procedures, and emotions and its utility in the determination of the pop up of a solution. LTM = long-term memory.

2001; Flykt, 2005; Öhman et al., 2001). The bulk of the evidence demonstrates that emotions can modulate attentional processes in the search of emotionally relevant targets. Attention is neurally implemented as a modulation of the neural signal so as to favor one type of item on another. Attention is not depending on a single brain region and as such can be understood as a component of the bottom-up and top-down dynamics that regulate object recognition processes. Procedural knowledge also has been characterized as a neural structural modification, and these procedure might be linked to declarative or perceptual cues (Kassubek, Schmidtke, Kimmig, Lücking, & Greenlee, 2001; Lindquist & Guadagnoli, 2008; Meister et al., 2004). Motor procedural knowledge, for example, reflects the changes in motor areas that take place after each training session. Hence, in an expert pianist, the sight of the notes immediately activates motor patterns (Meister et al., 2004).

Discussion

It is now widely recognized in the scientific community that intuition is a genuine phenomenon. Several theories have aimed to provide explanations for it, the theories put forward by Simon and colleagues (e.g., Larkin et al., 1980a; Prietula & Simon, 1989; Simon, 1989; Simon, 1995), on the one hand, and Dreyfus and Dreyfus (1988), on the other, have been the most influential. More recently, we put forward a new theory that, to some extent, integrates the strengths of these two theories (Gobet & Chassy, 2008, 2009). However, to this point, no theory has provided a detailed account of intuition at the biological level, spanning the neural and systems levels. The goal of the current paper was to provide such a theory, by showing how Hebb's (1949) concept of a cell assembly together with neural plasticity can be used to offer biological mechanisms for the concepts of chunks (Chase & Simon, 1973; Miller, 1956) and templates (Gobet & Simon, 1996b).

By using and developing the concept of cell assembly, we showed how advantageous it is for the brain to process information in a sequence of stages, each operating in parallel. The neural networks responsible for recognition are continuously reorganizing themselves so as to be able to increase the number of objects that can be recognized. Thus, insofar as the information is encoded within this network, the target object will be recognized in a few hundred milliseconds, whatever its level of visual complexity. Then, access to object-relevant information is processed nearly instantaneously, in another single step. The density of the network explains the striking rapidity with which experts spot the key features in a problem situation. The high speed with which the process takes place may lead to the conclusion that intuition is immediate. However, the processes take a few steps that are reflected in the various components of the EEG records (Eimer, 2000; O'Rourke & Holcomb, 2002). The fact is that learners are continuously reorganizing their neural network to capture the visual properties of an increasing number of possible objects. When objects belong to a single domain of expertise, they carry properties that characterize their relation to other objects of the domain (e.g., chess pieces and their spatial interactions). Learners first become skilled at recognizing objects. Then they pair objects with their properties—a process that enables the learner to assimilate features of the environment. Then, learners create links at a more abstract level; for instance, how maneuvers involving pieces interact with strategic features. This restructuration in turn will lead to the search for new visual cues aiming to confirm the existence of the links. Expert intuition is thus the result of a long learning process and reflects the density and plasticity of the networks linking unsupervised perception to high-level, supervised cognition.

It is worth noting that emotions influence the cognitive system twice. The first form of influence is when emotions accelerate memory encoding because the item has a particular emotional relevance. For example, after a game, chess players usually engage in a post mortem analysis to understand each phase of the game and exchange ideas. The player who has lost tries to isolate the opponent's maneuvers that took advantage of specific weaknesses. As they are associated with very negative emotions, these maneuvers are likely to remain in memory and be easily retrieved for a long time. The second influence of emotion comes when it directs attention toward potential emotionally loaded material (e.g., threats in chess). The key point is that emotions alter the activity of cell assemblies coding for objects of potential interest in the situation, and thus change the probability for an object to be activated and thus enter working memory. This modulatory influence of emotions is of central importance as it directs the way the perceiver builds an internal representation of the situation problem.

An incremental neural-network algorithm that provides some parallels with CHREST is Grossberg's (1976) adaptive resonance theory (ART). ART computer simulations have been successful in modeling perceptual and memory processes (e.g., Carpenter, & Grossberg, 1987; Carpenter, Grossberg, & Rosen, 1991). At the core of ART (e.g., Carpenter, & Grossberg, 1987), lies a memory store in which the input pattern is matched with an internal memory. This active cognitive device determines the subsequent course of actions. The coding of the input has varied in ART models, for example binary (Grossberg, 1987) and analog (Carpenter & Grossberg, 1987). CHREST uses list structures as input, a symbolic format.

ART addresses the stability-plasticity dilemma faced by all learning algorithms by providing both localized and distributed representations. Retrieval of information from an ART network results in a single, localized concept; with CHREST, this is a node. The information stored in a concept is distributed, rather than list-like in a CHREST node. Hence, modifying a concept, to reflect new information, can affect the complete set of stored information about a concept. Another difference is that ART assumes a parallel mode of processing, seeking out the most similar concept to the current input from the entire contents of its memory; CHREST instead works through a discrete set of tests, and only the retrieved node is compared with the input.

The theoretical framework proposed in the current paper argues that perceptual input is directly filtered by LTM knowledge; STM is not required for the process of intuition formation (as shown in Figure 5). This view is consistent with an MRI experiment showing that pattern recognition does not require anything else than automatic processing of perceptual input and LTM knowledge. The architecture of ART2 (Carpenter & Grossberg, 1987) implies that STM is necessary for new items to be stored, a view similar to that of Shiffrin and Atkinson (1969). This assumption does not stand close scrutiny for the molecular evidence shows that STM and LTM formation do not necessarily rely on similar molecular mechanisms. LTM requires proteins synthesis whereas STM does not. Furthermore, there is a substantial evidence that short- and long-term forms of memory are separable entities as evidenced by the molecular pathways underlying processing (Izquierdo, Medina, Vianna, Izquierdo, & Barros, 1999) and by animal data (Morice et al., 2008). Although accounting well for phenomena such as classification of patterns, ART-based models do not mention the influence of emotions on cognition. Finally, ART models do not account for intuition.

Our theory makes a strong prediction as to how intuition orients behavior from a cognitive point of view: Only the perceptual/memory areas should be active when experts solve simple problems. (By contrast, novices are predicted to engage frontal areas, known to engage processes such as planning and deliberate decision making.) This hypothesis can be tested with fMRI studies. In such experiments, it would be essential to know the exact level of expertise of the participants, as this directly relates to properties of the neural networks that will be solicited to carry out the task. As in previous research on expertise, chess would seem to be an ideal task environment, as competitive chess players have a rating that provides a reliable indicator of their strength. In addition, chess makes it easy to use problem-solving tasks, such as detection of checkmates, that are ecologically valid.

The contribution of this paper is to have provided a biological implementation for a theory of intuition previously expressed at a psychological level only. Just as the explanation at the psychological level, the explanation at the biological levels provides mechanisms for the key aspects of intuition. It explains the rapid and perceptual nature of intuition, its unconscious character, how it links to emotions, and its holistic character. Given that it assumes that chunks and thus expert intuition are the product of years of experience, the theory also explains why intuitions are more likely to provide correct solutions as expertise grows. It also leads to testable predictions. If, as we argued, intuition lies at the root of expertise, the mechanisms we advanced in this paper should shed light not only on the biological basis of intuition, but on the biological basis of expertise in general as well.

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