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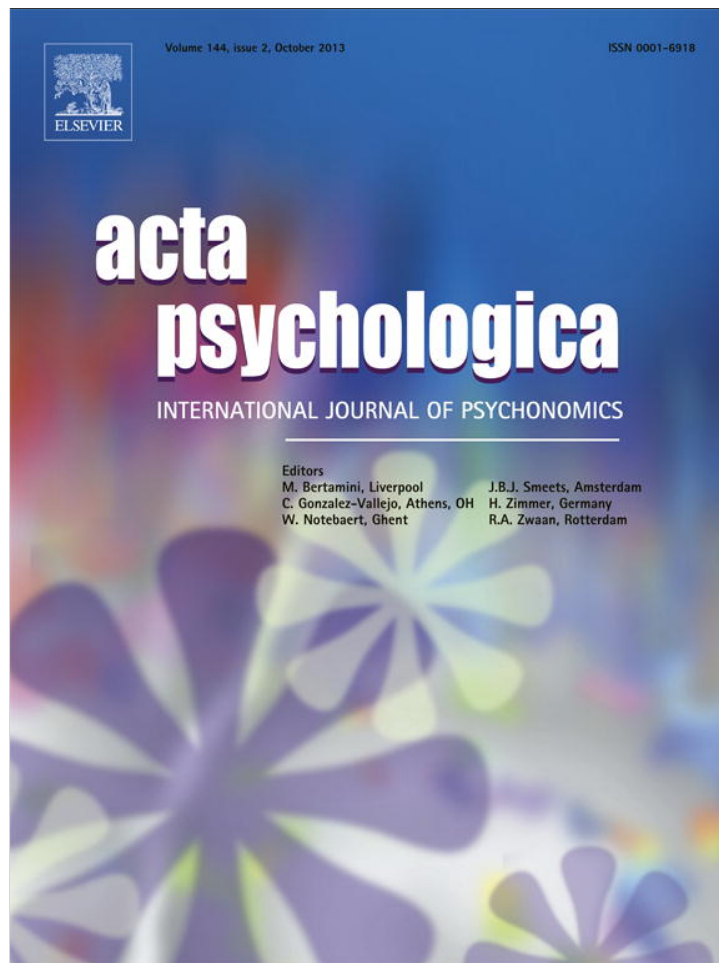Craddock, Paul
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Spatial integration of boundaries in a 3D virtual environment ☆

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ABSTRACT

Prior research, using two- and three-dimensional environments, has found that when both human and non-human animals independently acquire two associations between landmarks with a common landmark (e.g., LM1–LM2 and LM2–LM3), each with its own spatial relationship, they behave as if the two unique LMs have a known spatial relationship despite their never having been paired. Seemingly, they have integrated the two associations to create a third association with its own spatial relationship (LM1–LM3). Using sensory preconditioning (Experiment 1) and second-order conditioning (Experiment 2) procedures, we found that human participants integrated information about the boundaries of pathways to locate a goal within a three-dimensional virtual environment in the absence of any relevant landmarks. Spatial integration depended on the participant experiencing a common boundary feature with which to link the pathways. These results suggest that the principles of associative learning also apply to the boundaries of an environment.

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1. Introduction

Spatial integration refers to an organism's capacity for linking independently acquired spatial information that shares a common element. Ellen, Soteres, and Wages (1984) provided one of the first observations of such a phenomenon. They showed that rats were able to integrate individually and separately acquired spatial relationships into a unified cognitive representation. Such an integration of fragmentary maps into a whole map should allow an organism to follow the direct route from one part of the environment to another (Gallistel, 1990; Poucet, 1993; Worden, 1992). This ability is one basic tenet of the cognitive map theory proposed by Tolman (1948) and developed by O'Keefe and Nadel (1978). The latter proposed that a cognitive map allows organisms to conceptually link parts of an environment that have never been experienced at the same time (O'Keefe & Nadel, 1978).

A growing body of literature suggests that spatial integration is ruled by associative mechanisms of high-order conditioning (Leising & Blaisdell, 2009). A classic example of high-order conditioning is sensory preconditioning (SPC, Brogden, 1939). A conventional SPC procedure consists of pairing two neutral stimuli (S2–S1) in Phase 1 and then pairing S1 with an unconditioned stimulus (US; S1-US) in Phase 2. When testing S2, a conditioned response (CR) appropriate to the US is observed, even though S2 itself has never been paired directly with the US. The same result (i.e. a CR to the S2) is observed following a second-order conditioning procedure (SOC; Pavlov, 1927) that consists of an SPC procedure with Phases 1 and 2 reversed. Within the timing literature, Miller and colleagues provided evidence that the integration of temporal maps is based on the associative process of SPC (see Savastano & Miller, 1998 for a review). For example, Matzel, Held, and Miller (1988) initially trained rats with S2–S1 pairings with a trace interval followed by backward pairings of S1 with an aversive US (i.e., US-S1). Conditioned responding was not observed following presentation of S1 (consistent with the backward conditioning response deficit; Pavlov, 1927). However, S2 evoked strong conditioned responding. The authors interpreted this result as indicative of temporal integration of associative memories acquired during Phase 1 and 2 of training that shared a common element (S1). Through temporal integration, the rats seemingly retrieved a representation of the US upon presentation of S2. Leising, Sawa, and Blaisdell (2007) reported similar findings in an appetitive conditioning procedure with rats. In addition to Matzell et al.'s (1988) findings on SPC, Miller and colleagues reported a few years later evidence for temporal integration in second-order conditioning (SOC; e.g., Barnet, Cole, & Miller, 1997; Barnet & Miller, 1996; Cole, Barnet, & Miller, 1995).

Within the spatial literature, Sawa, Leising, and Blaisdell (2005) explored the integration of spatial maps in a two-dimensional spatial-search task presented on a touchscreen to pigeons. In phase 1, pigeons

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were presented with two visual landmarks (X and A) that had a consistent spatial relationship to each other. The pigeons were then reinforced for pecking at an unmarked goal location, which bore a constant spatial relationship to first-order A, which was presented in the absence of X. Subsequent test trials on which X alone was presented revealed that the pigeons were able to infer a spatial relationship between X and the goal (seemingly, an X-A-goal associative chain). This suggests that pigeons have the ability to combine two independently learned spatial maps into a single spatial map by a common linking element (i.e., A) in a two-dimensional setting. Using an open-field procedure with pigeons, Blaisdell and Cook (2005) reported spatial integration similar to that found by Sawa et al. (2005). Similarly, Molet, Jozefowiez, and Miller (2010) showed integration, in humans, of independently acquired spatial relationships in a 2-D, computer, landmark-based search task. Using a dynamic 3-D virtual environment, Molet, Bugallo, and Gambet (2011) extended this result by providing evidence that humans can integrate two spatial relationships between landmarks into a new spatial relationship that guides spatial navigation.

Data in the literature supportive of spatial integration in two-dimensional environments with pigeons and humans (Molet et al., 2010; Sawa et al., 2005), in conjunction with results observing spatial integration in three-dimensional environments with pigeons and humans (Blaisdell & Cook, 2005; Molet et al., 2011) support the hypothesis that the processes that integrate information concerning separate but related associations between landmarks when using spatial information work in a way that is similar to the processes involving temporal information in experiments from the timing literature (e.g., Savastano & Miller, 1998).

While these studies focused on landmark-based spatial learning, Prados, Alvarez, and Reynolds (2011) provided evidence suggesting that spatial integration could be extended to geometric cues and compound stimuli containing both geometric and non-geometric information, by using SOC and SPC procedures in a 2D computer based search task with humans (see also Rhodes, Creighton, Killcross, Good, and Honey (2009) for a similar experiment in rats). However, a closer look at their data reveals that the evidence is rather modest. In Experiment 2 (SOC), two groups of participants (Experimental and Control) first learned to use triangle shapes to locate a goal. Subsequent to this, the Experimental group received compound exposure in which the trained triangle was associated with a second triangle for a number of trials. The two triangles were aligned such that the vertex indicating the goal in one triangle (CS1) overlapped with the other (CS2); whereas the Control group did not receive any compound exposure. During testing with CS2, both groups were tested with an untrained triangle. The participants choosing the vertex that overlapped with CS1 indicated integration, whereas, those choosing the vertex that matched the reinforced angle of CS1 from training indicated generalization. Though more participants chose a strategy based on integration in the Experiment group (30%) in comparison to the Control group (10%), the data revealed that the dominant strategy adopted by the participants in both groups was not integration but rather generalization (50% in the Experimental group and 70% in the Control group). The integration strategy was indicated when the choice occurred as if the participants inferred the spatial relationship between the untrained triangle and the goal through the trained triangle from Phase 1. The generalization strategy was indicated when the choice occurred as if the test-trial triangle was the trained triangle from Phase 1 (see also Sawa et al., 2005, for a similar result in pigeons). Experiment 4 (SPC) that reversed the order of place preference training and the compound exposure training phases reproduced the results observed in Experiment 2.

The data reported by Prados et al. (2011) provide some indication that spatial integration between geometric cues is possible; yet leave a need for more solid demonstrations that minimize generalization effects. First, it would be more convincing to observe that spatial integration is the dominant strategy. Second, it would be more relevant to observe spatial integration of geometric cues in a three-dimensional environment to mimic real-world situations. This is potentially important because real-world events involve physical settings that often differ from one another by geometry that can be used in spatial navigation. Some have argued that geometric features of the environment are processed with a dedicated geometric module that utilizes specific rules that differ from those governing landmark-based learning (Cheng, 1986; Döeller & Burgess, 2008; Gallistel, 1990). Even though doubt has been cast upon this geometric module hypothesis (Cheng, 2008; Pearce, 2009), the idea from which it originated, that geometric features of the environment should be of a greater biological importance for organisms than landmarks, is not inconsistent with an associative analysis of spatial learning (Miller & Shettleworth, 2007).

According to the cognitive map theory, there is a clear distinction between the taxon system, based on associative learning, and the local system, based on place learning (O'Keefe & Nadel, 1978). These two systems make reference respectively to what Tolman (1948) called the narrow strip-map, and the broader and more flexible comprehensive map. The discovery of place cells, hippocampal neurons that increase firing rate only at a particular location of the animal environment (O'Keefe & Dostrovsky, 1971), led to the assumption that the hippocampus is the neural substrate of the cognitive map (O'Keefe & Nadel, 1978). At that time, progress in neuroscience reinforced the hypothesis of two neural systems dedicated to spatial learning, the hippocampus being allocated to the local system, while the extra-hippocampal areas being involved in the taxon system. One major distinction between these two systems lies in the fact that, unlike the taxon system, the local system is involved in situations where landmarks are absent or made unusable. The local system is also known to automatically update new information of the explored environment into the cognitive map, while the taxon system is subject to cue-competition phenomena. A recent two-system account of spatial learning comes from Burgess (2006, 2008) who posits that allocentric spatial coding, that is to say the local system, is limited to the boundaries of the environment, whereas egocentric coding, that is to say the taxon system, is allocated to associations between the animal and landmarks of its environment. From an associative learning perspective, the rules involved in spatial learning based on boundaries or shapes of the environment, and the rules that govern landmark-based spatial learning should be the same, so that spatial integration without any landmark should also follow associative learning rules.

The aim of the present research was to assess the possibility of spatial integration in a navigation task, following associative learning principles with the geometric information of a virtual maze as the only available and relevant stimulus. In Experiment 1 (using SPC) and Experiment 2 (using SOC), we asked whether human participants would be capable of integrating separately learned geometric information to locate a goal within a three-dimensional (3D) virtual environment.

2. Experiment 1

The participants were assigned to one of two groups: Common Element and No Common Element. The Common Element group assessed the potential integration of spatial relationships sharing common elements between learning Phases 1 and 2. The No Common Element group served as a control condition that precluded integration of spatial relationships by not having common elements between Phases 1 and 2 of learning.

Both groups explored a 3D virtual environment modelled on a kite-shaped maze by using an SPC procedure (see Fig. 1). They first explored two separate pathways (A and X, see Fig. 2, screenshots 3 and 4 respectively) that both originated from a starting room (see Fig. 2, screenshots 1 and 2), and ended in two different adjoining rooms (B and Y, see Fig. 2, screenshots 5 and 6 respectively). A and X can be easily discriminated by the spatial relationship they share with the starting room. More specifically, when the participants start in the starting room, the entry of A is always at the left corner, providing a left diagonal path, while the entry X is always at the right corner,
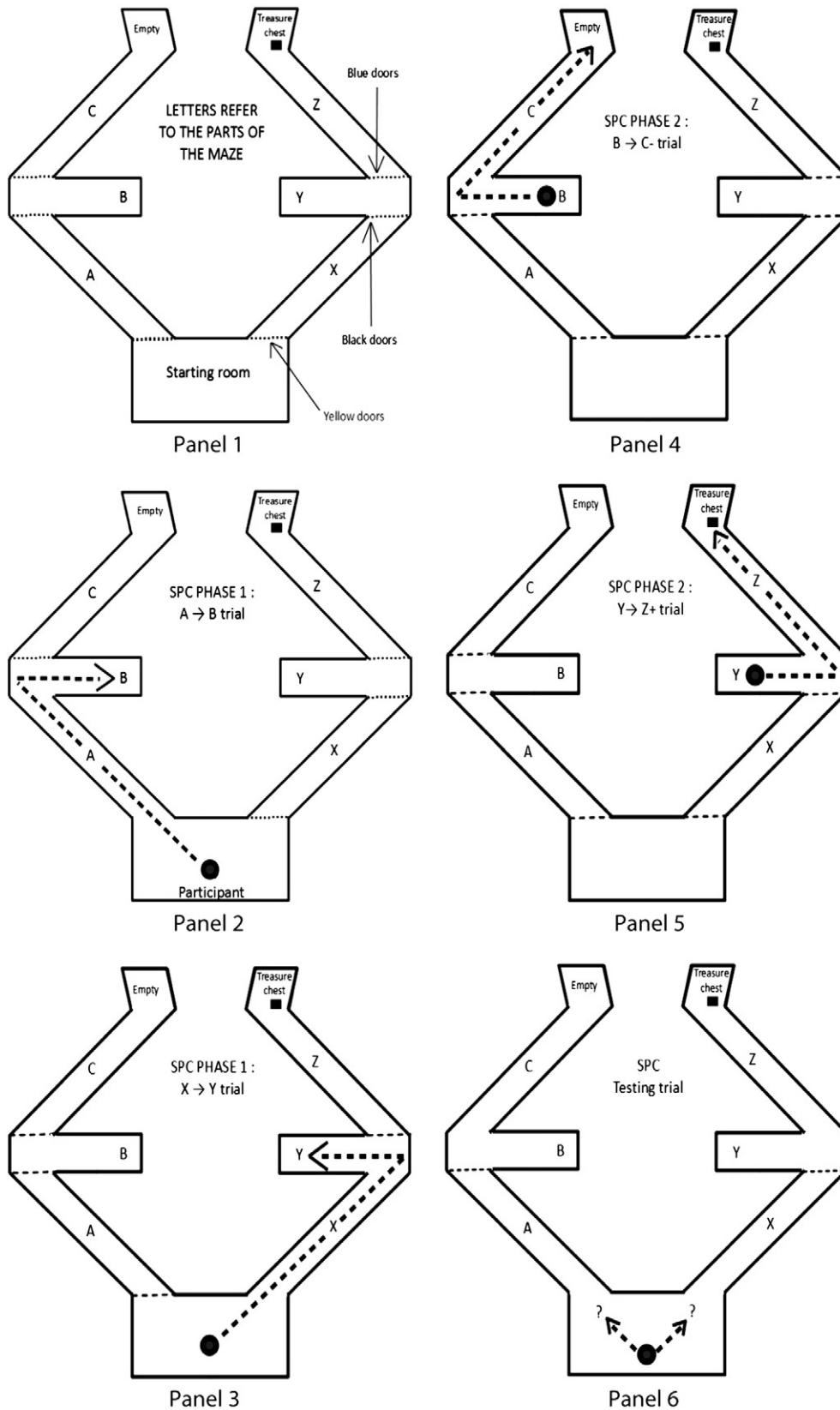
Fig. 1. Schematic representations of the virtual environment used in the present research (never seen by the participants). The colors of the doors are symmetrically identical.

providing a right diagonal path. The symmetrically opposite spatial relationship between the first alleys (A and X) and their adjoining rooms (B and Y respectively) constitutes the crucial information that emerges from the boundaries of the walls and the angles they form.

In Euclid terms, a boundary can be defined as the extremity of anything and the angles as an inclination of two lines in a plane which meet one another and do not lie in a straight line (Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012). We hypothesized that navigation

through these parts of the maze would automatically elicit the formation of two spatial associations of the environment (i.e., A → B and X → Y). Subsequent to this, the participants in the Common Element group explored two additional pathways (C and Z, see Fig. 2, screenshots 7 and 8 respectively) that each originated from their respective adjoining rooms (i.e., B and Y) and ended in two different goal rooms. The path Z led to a room containing a treasure chest ($+$) whereas the path C led to an empty room ($-$) (see Fig. 2, screenshots 10 and 9 respectively). The color of the walls and doors of rooms B and Y were exactly the same. The only available cue to discriminate between these two rooms was the position of the sharp angles formed by the connecting rooms (B and Y) with the final pathways (C and Z), from the starting position of the participants during this second Phase. Although unnecessary to this discrimination, the differently colored doors could have also been used to disambiguate the two rooms B and Y. When starting in room B, the black door was on the left and the blue one on the right, contrary to the room Y. It is worth noting that alone, associations between colors could not have been used to resolve the task, since the association chains were the same for the two possible pathways of the maze (i.e. Yellow → Black → Blue → Empty and Yellow → Black → Blue → Treasure chest). Back to the starting point, the participants were then asked to take the route that led to the treasure. If participants in the Common Element group integrated the independently learned geometric information of their environment by means of the common elements (i.e., adjoining rooms B and Y), then one would expect them to take the path X to reach the room containing the treasure chest despite the fact that the two pathways X and Z had never been experienced through a continuous exploration. We hypothesized that this result would reflect the establishment of two associative chains: X → Y → Z$+$ and A → B → C$-$.

The participants in the No Common Element group also explored two additional pathways (C and Z) that ended in two different goal rooms. The path Z led to a room containing a treasure chest ($+$) whereas the path C led to an empty room ($-$). However, they did not originate from the adjoining rooms (i.e., B and Y). Instead, they started at the bottom end of Pathway C or Z. In test, it was expected that participants in the No Common Element group would not integrate the independently learned geometric information because no common elements (i.e., no adjoining rooms B and Y) were experienced in the second phase to connect the learned information with the first phase.

2.1. Method

2.1.1. Participants

Thirty-two students from the University of Lille, between 18 and 30 years old and without any previous experience with this task participated in Experiment 1 (16 women and 16 men). They were randomly assigned to one of two groups (Common Element and No Common Element, both n = 16) with an equal sex ratio.

2.1.2. Apparatus

The experiment was conducted in a cubicle containing a table, a chair, and a computer for the participant placed in the centre of the cubicle. The dynamic 3D virtual environment was implemented using the 3DVIA Virtools software (Dassault Systemes).

The 3D virtual environment consisted of a kite-shaped maze (see Panel 1 in Fig. 1). Dimensions of length × width × height were measured in virtual units (vu). The starting room (40 × 20 × 10 vu) was flat gray in color with dark walls and was connected to two pathways (A and X; 60 × 10 × 10 vu each). Each pathway was identical, with blue walls and a dark red floor; and was separated from the starting room by a yellow door that was either open or closed. Pathway A led to Room B (26.5 × 10 × 10 vu) through a black door, and Pathway X led to Room Y (26.5 × 10 × 10 vu) also through a black door. It took approximately 5–6 s to reach the end of Room B or Y from the

starting point in a straightforward journey. Rooms B and Y are also described as the small rooms in the text due to their small dimension. A blue door separated Room B from Pathway C (60 × 10 × 10 vu) that led to a goal room (10.7 × 7.5 × 10 vu) with a treasure chest (5 × 5 × 5 vu). In like manner, Room Y was separated by a blue door from Pathway Z (60 x 10 x 10 vu) that led to the second goal room (10.7 × 7.5 × 10 vu). It took approximately 4–5 s to reach the end of the Room B or Y from the starting point in a straightforward journey. The adjoining rooms B and Y were identical: both had white walls and dark red floors. Both end rooms were also identical, with yellow walls and dark red floors. All doors could either be open or closed (the thick dark lines in Panel 1 of Fig. 1 indicate that the door is closed). For half of the participants the goal room on the right contained the treasure and for the remaining half it was reversed. For the sake of clarity, only the condition in which the treasure was placed in the room on the right will be further described.

2.2. Procedure

Participants moved through virtual space by pressing keyboard keys: ↑ (forward), ↓ (backward), ← (left rotation), and →(right rotation). Participants navigated from a first-person perspective, at a constant velocity. The computer screen displayed a view from the perspective of the participant within the 3D virtual environment so that the arrangement was analogous to an individual's view of the natural environment (see Fig. 2).

Participants were run individually. The experiment was conducted in 3 phases.

2.2.1. Training phase 1

Phase 1 consisted of a semi-randomized sequence of three A → B trials and three X → Y trials (see Panels 2 and 3 in Fig. 1) that were counterbalanced across participants for order. Before start, the participant was presented the following information (screen 1) "You will always be in the same maze throughout the experiment. You can move by using the arrow keys of the keyboard. Press SPACEBAR to continue…" (screen 2) "For the moment, only one part of the maze will be open to you. You will start from the starting room. For each trial, only one of two paths will be available. Your task is to walk along the open pathway from the starting room to the end. There will be several trials to explore your environment. Press ENTER to continue…" After reading and responding, half of the participants began the first trial with Pathway A being the only available pathway. A closed door blocked the entrance to Pathway X. The trial ended when the participants reached Room B. The next trial began with the participants being repositioned in the starting room with Pathway A being closed and Pathway X that led to room Y being open. This trial ended when the participants reached room Y. The doors separating Room B and Room Y from Pathways C and Z were closed during this phase. For the remaining participants the trial order was reversed.

2.2.2. Training Phase 2

During Phase 2, participants were assigned to one of two conditions: Common Element and No Common Element. The Common Element condition consisted of a semi-randomized sequence of three B → C$-$ trials and three Y → Z$+$ trials (see Panels 4 and 5 in Fig. 1) that were counterbalanced across participants for order. Before start, the participant was presented the following information "From now on, the blue doors will be open. The unexplored part of the maze is available to you. You will now start from the small rooms. For each trial, only one of two paths will be available. Explore the pathway that is open until you reach its end. Press ENTER to continue…" After reading and responding, half of the participants began the first trial in Room B where only Pathway C leading to the left goal room was open. A black door blocked the exit to Pathway A. Participants were verbally instructed to make a 360° rotation before the first trial.
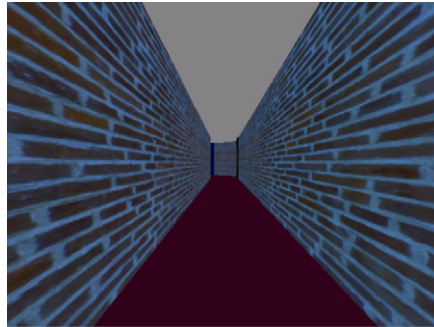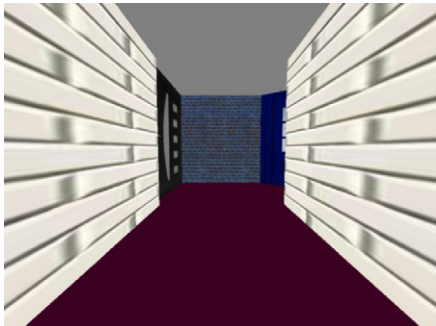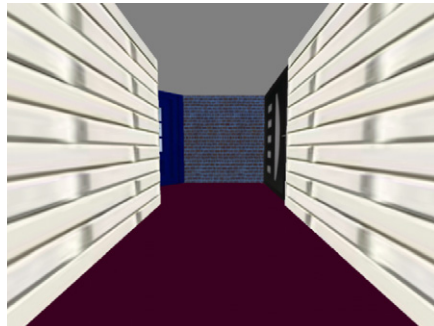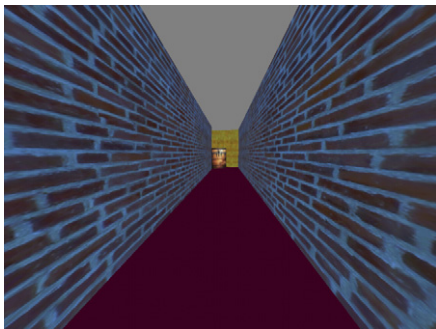
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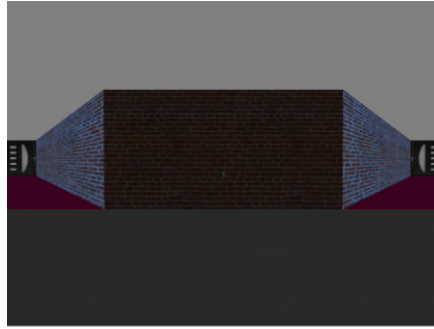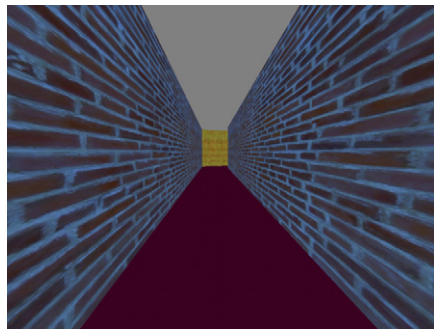
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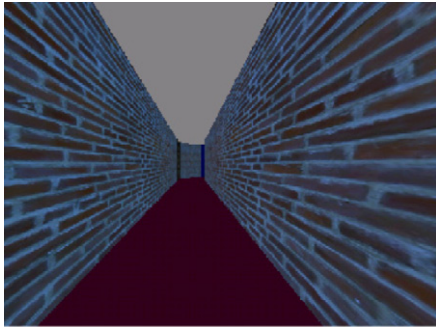
Screenshot 3

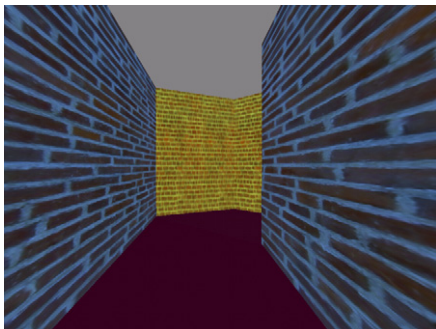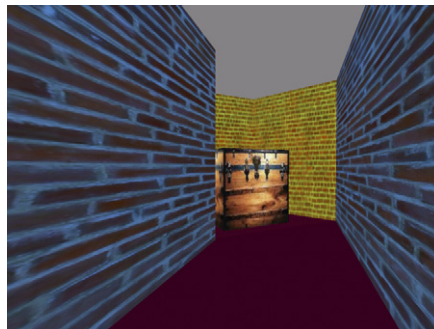Screenshot 4

Screenshot 5

Screenshot 6

Screenshot 7

Screenshot 8

Screenshot 9

Screenshot 10

When the participants reached the empty goal room an aversive sound corresponding to the opening of an empty treasure chest in Zelda's, Ocarina of Time (Nintendo) was produced. The next trial began by repositioning participants in Room Y with Pathway Z being open and the exit to Pathway X being blocked by a closed door. When participants reached the right goal room containing the treasure chest a pleasant sound (corresponding to the discovery of a treasure in Zelda's, Ocarina of Time) was produced as reinforcement.

In the No Common Element condition, participants started at the bottom end of Pathway C or Z, the blue doors separating these pathways from the small rooms being closed. Thus the participants in the No Common Element condition did not experience the adjoining rooms (B and Y). This was the critical difference with the Common Element condition that was expected to preclude integration of spatial relationships. Their task was to progress along the pathway until they reached the goal room. Participants explored the last part of the maze through a semi-randomized sequence of three C− trials and three Z+ trials that were counterbalanced across participants for order. The instructions were adapted as follow: "The unexplored part of the maze is available to you. For each trial, only one of two paths will be available. Explore the pathway that is open until you reach its end. Press ENTER to continue…"

2.2.3. Test trial

Before completing the test trial the following instructions were displayed on the screen, "The entire maze is now available, and you have the key that allows you to open the treasure chest and discover its contents. You will start from the starting room of the maze. To open the closed doors, you have to press SPACEBAR. But, CAREFUL!! Once you make a choice, you cannot go back. There is no time limit. Press ENTER to start." Once the instructions were understood, participants found themselves in the starting room and were allowed to choose between opening one of the two doors (see Panel 6 in Fig. 1).

2.3. Results and discussion

The majority of the participants in the Common Element group (14 out of 16, 87.5%) chose to take the pathways leading to the treasure. This result was anticipated on the basis of the integration of spatial relationships between pathways $X \to Y$ and $Y \to Z+$, and between pathways $A \to B$ and $B \to C-$. A binomial test indicated that this was significantly different from chance (50%), $p = .005$. In the No Common Element group, only 6 out of 16 participants (37.5%) made the same choice. A binomial test indicated that this was not significantly different from chance (50%), $p = .4$. The Pearson Chi-square test also supported the finding that the choice strategy significantly differed between groups χ^2 (1, 32) = 8.53, $p = .003$ (Cramer's V = 0.52, $p = .003$). The results of this study provide clear evidence that human participants have the ability to integrate two separate experiences with spatial geometry when boundaries overlapped. The integrated spatial information presumably resulted in a unified higher-order spatial map that was based on the superimposition of the associations in memory that shared common elements (rooms B and Y). Importantly, the use of intra-maze cues to resolve the task was neutralized since the two pathways of the maze were identical. Moreover, no extra-maze cue was present. It is worth noting that while instructions in the present experiment, (i.e., "you will always be in the same maze throughout the experiment"), might have increased attention to common and overlapping spatial features of the maze, this directed attention was not sufficient to produce spatial integration. Rather, actual experience of the common, overlapping

features (rooms B and Y), was necessary for participants to show evidence of higher-order integration at test (as in the Common Element group but not the No Common Element group). Importantly, all participants were interviewed after completion of the experiment, and none of the participants that showed spatial integration were able to clearly verbalize the reasons for his/her choice (i.e., use of a spatial integration strategy). Therefore, responding presumably depended on simple associations that encoded spatial relationships rather than on higher-order cognitive processes based on the use of linguistic labels such as "left and right". As far as we know, this is the first clear demonstration of spatial integration of boundaries of a three-dimensional environment in a human navigation task, without any relevant landmark.

3. Experiment 2

Given the similarity of the procedures for SPC and SOC, it appears highly plausible that the spatial integration of boundaries of an environment also applies to SOC. However, there have been some reports questioning the similarity of the underlying associative structures of SPC and SOC (e.g., Rizley & Rescorla, 1972). As opposed to the SPC procedure of Experiment 1 in which participants learned the maze's parts separately in a forward pattern (i.e. exploring the first part, and then the last part of the maze), the SOC procedure of Experiment 2, assigned the participants to a backward pattern (i.e. exploring the last part before the first part of the maze). Hence, we sought to investigate the generality of the findings of Experiment 1 by determining whether a SOC procedure would also indicate spatial integration of boundaries of the environment. The design was identical to that used in Experiment 1 with the exception that Phases 1 and 2 were reversed.

3.1. Method

3.1.1. Participants

Thirty-two students from the University of Lille, between 18 and 30 years old and without any previous experience with this task, participated in Experiment 2 (16 women and 16 men). They were assigned to one of two groups (Common Element and No Common Element (both n = 16) with an equal sex ratio.

3.1.2. Apparatus and procedure

The apparatus and procedure were the same as those used in Experiment 1 except that Phases 1 and 2 of training were reversed.

3.2. Results and discussion

The results of Experiment 2 extend the results of Experiment 1. The majority of the participants in the Common Element group (13 out of 16, 81.25%) chose the correct pathway that led to the treasure. A binomial test indicated that this was significantly different from chance (50%), $p = .02$. In the No Common Element group, only 7 out of 16 participants (43.75%) made the same choice, which did not differ significantly from chance (50%), $p > .8$. The Pearson Chi-square test revealed that the choice strategy significantly differed between groups χ^2 (1, 32) = 4.80, $p = .03$ (Cramer's V = 0.39, $p = .03$). We interpret this result as indicative of spatial integration of associations acquired during Phase 1 ($Y \to Z+$; $B \to C-$) and Phase 2 ($X \to Y$; $A \to B$) of training based on the element common to both experiences (i.e., Y; B). Through spatial integration, the participants seemingly retrieved a representation of X as the pathway leading to the treasure.

Fig. 2. Screenshots from the first-person perspective within the 3D virtual environment taken at each part of the maze.. Panels 1 and 2 have been taken at the beginning of phase 1 and test phase respectively, in the starting room. Panels 3 and 4 have been taken in the entrance of alleys A and X of phase 1. Panels 5 and 6 have been taken in the beginning of phase 2 (experimental group), respectively in room B and Y. Panels 7 and 8 have been taken in the 2nd phase, in the entrance of alleys C and Z respectively. Panels 9 and 10 have been taken at the end of the second phase, when participants face the end rooms of alleys C and Z respectively. In this condition, the treasure was at the end of alley X, as in Fig. 1.

This is consistent with the idea that participants encoded associative chains X → Y → Z + and A → B → C −.

4. General discussion

We found evidence in both SPC and SOC that human subjects navigating a virtual maze can integrate separately learned geometric information that are joined by a common element, in a landmark-free environment (i.e. with neutralized extra-maze and intra-maze cues). The unique nature of the SPC and SOC procedures used in the present navigational task involving pathways and small rooms deserve attention, as it differs from previous research relying on discrete stimuli. Our demonstrations of spatial integration using a navigation task with boundaries of a 3D environment as the only available stimuli are readily explained by high-order associative principles, and argue against the claim that the rules governing geometric information are different from those governing landmark-based spatial learning (Cheng, 1986; Döeller & Burgess, 2008; Gallistel, 1990). The results we report here extend associative learning theory to situations involving spatial integration of boundaries of the subject's navigational 3D environment, which is consonant with the growing evidence that associative learning can be conceived as a general theory of learning (Pearce, 2009). Our results also add to the growing body of work revealing a role of associative processes in integrating spatial information across separate experiences (Blaisdell & Cook, 2005; Chamizo, Rodrigo, & Mackintosh, 2006; Leising, Sawa, & Blaisdell, 2012; Sawa et al., 2005).

As animals have to navigate through the same environment in different seasons, the general shape of the environment is important. It is, after all, more likely to remain constant, while physical information (e.g. color or texture) is more likely to change. Gallistel (1990) proposed this hypothesis to theoretically justify the claim that the brain contains a geometric module capable of only processing geometric information (Cheng, 1986; Gallistel, 1990). Recently, Prados et al. (2011) challenged this view but, as we mentioned in the introduction, the demonstration was modest. Nevertheless, his results suggested that (1) geometric information can interact with non-geometric information (Experiment 1 and Experiment 3) and that (2) spatial integration could be extended to geometric cues by means of SOC (Experiment 2) and SPC (Experiment 4) procedures in a 2D computer based search task with humans. We extended these findings by using a 3D environment without any discriminative landmarks, and evidencing spatial integration that more closely resembles real-world situations where the most relevant information for reaching a goal is provided by the boundaries of pathways in a given environment. This is particularly important in humans, as boundaries or shapes of streets are less likely to change than building facades that can quickly and unpredictably be renovated and repainted. Consonant with this idea, empirical evidence of the primacy of extended surfaces over landmarks has been found in human children under 5 years of age and in rats (see Tommasi et al. (2012), for a review). Moreover, it has been shown in rodents that neurons in the hippocampus (O'Keefe & Burgess, 1996; Wills, Lever, Cacucci, Burgess, & O'Keefe, 2005) and the medial enthorinal cortex (Barry, Hayman, Burgess, & Jeffery, 2007; Fyhn, Hafting, Treves, Moser, & Moser, 2007) are strongly responsive to the macroscopic surface layout of an environment, suggesting a primacy in the treatment of geometric information. The fact that physically disparate stimuli are processed in different neural networks, also called neural modules, has been used to suggest a modularity of learning rules (Jeffery, 2010). That said, it deserves noting that Pecchia and Vallortigara (2012) demonstrated that chicks rely solely on discrete objects to find a reward site in a rectangular shaped arena. Their performance was not different than chance as soon as they were provided only with the geometric information of the arena. This discrepancy might be explained in terms of stimulus saliency, which could be the determinant factor for using only one

type of information (i.e. geometric or non-geometric information) when both are available. Such an assumption remains to be experimentaly tested.

In support of the view that associative learning mechanisms have general applicability are all the studies that report evidence of temporal integration, a phenomena that has been extensively investigated by the Miller laboratory (see review by Savastano & Miller, 1998). For example, Arcediano, Escobar, and Miller (2003) trained human participants in a computer-based sensory preconditioning task. Subjects observed the temporal relations between visual cues presented on the screen. After viewing a sequence between A and B (A → B) in Phase 1, and a sequence between B and an outcome (B → O) in Phase 2, subjects were presented with event A and asked to press a key when they thought O would occur. Different groups of subjects experienced different temporal arrangements of events. Only those subjects for whom a linking element was common across the two phases showed temporal integration, and pressed the button most frequently at the time O would be predicted to occur based on temporal integration (see also Molet et al., 2010).

In addition to the encoding of spatial and temporal information between events, there is evidence that causal relationships or causal maps can be encoded and integrated during conditioning procedures. For instance, rats appear to be capable of learning cause-effect relationships between paired events, and of integrating them into a coherent causal map that guides causal inference (Blaisdell, Sawa, Leising, & Waldmann, 2006; Leising, Wong, Waldmann, & Blaisdell, 2008). The catalog of paradigms, procedures, motivational systems, and species in which spatial, temporal, and causal information are encoded and integrated suggests that associative processes are fundamental for binding together independently acquired perceptions and memories (Blaisdell, 2009).

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