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# The use of spatial reference cues and primary cue strategies for maze running by the desert tortoise, Gopherus Agassizii

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# THE USE OF SPATIAL REFERENCE CUES AND PRIMARY CUE STRATEGIES FOR MAZE RUNNING BY THE DESERT TORTOISE, GOPHERUS AGASSIZII

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A Thesis
Presented to the
Faculty of
California State University,
San Bernardino

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In Partial Fulfillment
of the Requirements for the Degree
Master of Arts
in
Psychology: General-Experimental

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by
Michelle Lee Eliker
June 1997

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# ABSTRACT

Observations of the desert tortoise in its natural habitat suggest that it possesses the ability to learn the location of important natural resources. Little research has been done, however, to determine which spatial cues are being used to determine these locations. Using controlled conditions, this study investigated the possible use of three spatial reference cues, odor, light, and landmark, by fifteen captive bred desert tortoises, aged 5 months to 3 years. The subjects were required to navigate a maze using 1 of the 3 cues to locate a food reward. After each subject was trained on all 3 cues separately in 3 learning sets, they were presented with the 3 cues simultaneously to determine if there was a preference for any cue. The hypothesis that the subjects would be able to use all 3 cues to navigate the maze for food, but with a preference for the landmark cue, was not supported. The results indicated that only the correct goalbox choices to the light cue had a significant increase from Increment 1 to Increment 12. Nevertheless, the tortoises did show a steady improvement across the increments for locating the reward using the landmark cue. The odor cue, however, did not appear to be employed by the tortoises to navigate the maze. The tortoises also did not appear to have a cue preference and they did not choose one cue significantly over another when presented with all 3 cues simultaneously. The finding that the subjects were capable of learning to use a specific cue to navigate the maze suggests that this cue might also be used by tortoises to navigate in their natural environment. This discovery could be meaningful to desert tortoise relocation efforts as knowing what cues are relied on for orientation will allow relocation sites to be chosen that will best meet this species' habitat requirements.

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To

Bilbo

Frodo

Merry

Pippin

Sam

Thorin

Oin

Gimli

Dori

Elrond

Legolas

Aragorn

Beorn

Boromir

Gandalf

and

Jimmy

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# INTRODUCTION

On April 2, 1990 The Department of the Interior, Fish and Wildlife Services provided a final rule listing of the desert tortoise, Gopherus agassizii, as a threatened species under the Endangered Species Act, as amended (ACT) (55 FR 12178 as cited in Federal Register, 1994). The ACT requires that critical habitat (CH) be established for all species listed as threatened or endangered to the greatest extent determinable and prudent. Regulations of the Service state that a CH can be determined only if there is sufficient data to perform the analysis necessary in evaluating the impact of habitat designation on species and human use. It is therefore critical that the biological needs of the species are known well enough so that a CH can be identified. The ACT defines CH as:

> (I) the specific areas within the geographic area occupied by the species . . . on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed . . . upon a determination . . . that such areas are essential for the conservation of the species (section 3[5][A] as cited in Federal Register, 1994).

The ACT defines conservation as "the use of all methods and procedures which are necessary to bring an endangered species or threatened species to the point at which the measures provided pursuant to this Act are no longer necessary" (section 3[3] as cited in Federal Register, 1994). While CH should encompass land crucial for the survival and recovery of the species, the ACT does not specify, and suggests that in most cases it is not necessary, that all areas of the species' habitat be included in the designation. The CH procedure outlined in the ACT is not a management or recovery plan but is a way to concentrate conservation activities in areas that contain the natural resources needed for the species' recovery.

Three components are evaluated by the Service when designating CH: "(I) the elements and areas essential for the species survival and recovery (II) the potential costs of the proposed areas and (III) what areas should be excluded due to economic and other impacts (50 CFR as cited in Federal Register, 1994)." The physical and biological considerations used in the service's determination include:

> (1) Space for individual and population growth, and for normal behavior;
> (2) Food, water, or other nutritional or physiological requirements;
> (3) Cover or shelter
> (4) Sites for breeding, reproduction, rearing of offspring; and
> (5) Generally, habitats that are protected from disturbance or are representative of the historic geographical and ecological distributions of a species. (50 CFR 424.12 as cited in the Federal Register, 1994)

The possible costs that could lead to exclusion of an area include negative impacts and infringement on private and tribal lands, economic effects on farming, livestock grazing, mining rights,and a consequence on recreational activities that affect the area economy.

By evaluating the species' habitat preferences, CH can be established so that the primary constituents for the species, such as sites that will support nesting, foraging, and adequate gene flow, are incorporated. Included in these considerations should be the seven principles of conservation biology used in the Draft Recovery Plan (58 FR 16691 as cited in the Federal Register, 1994) which are as follows:

> (1) Reserves should be well distributed across a species' native range;
> (2) Reserves should contain large blocks of habitat with large populations of the target species;
> (3) Blocks of habitat should be close together;
> (4) Reserves should contain contiguous rather than fragmented habitat;
> (5) Habitat patches should contain minimal edge to area ratios;
> (6) Blocks should be interconnected by corridors or linkages containing protected, preferred habitat for the targeted species; and
> (7) Blocks of habitat should be roadless or otherwise inaccessible to humans.

To establish these seven principles, it is critical that sufficient knowledge is obtained about a species' use of their environment. This study will examine the navigational abilities of the desert tortoise, specifically the effect of chemosensory cues, fixed point cues (landmarks), sun orientation, and the combination of these three cues, on the desert tortoise's ability to navigate within its environment.

Loosely defined, spatial orientation is an organism's "behavioral response to some stimuli" (Van Der Steen & Ter Maat, 1979). More specifically, spatial orientation is a response that determines an organism's posture and locomotion in space in reference to spatial cues (Schöne, 1984; Waterman, 1989). Locomotion is the behavioral response directed by navigation and begins with the basic orientation of the organism. For an organism to traverse its environment it must be oriented to the space around it. Orienting responses can be positional, stabilizing, or goal directed, which includes both distant and proximate orientation.

Positional orientation refers to the location and posture of an organism's body relative to space and permits the organism to maintain preference positions (Schöne, 1984), such as normal position, its subcategory equilibrium, and the rtat (CH) be esta Positional orientation reflects the relationship between the geometry of the body and the geometry of the environment (Waterman, 1989) and will vary between species. For most free-living species, positional orientations are based on a bilateral symmetry defined by three perpendicular axes, which include the rostro-caudal or anterior-posterior (X) axis, the transverse or right-left (Y) axis, and the dorsoventral (Z) axis that is the vertical axis (Schöne, 1984). These axes allow for three degrees of rotation, or a change in direction. Body rotation around the X axis is called roll, pitch refers to rotation around the Y axis, and yaw is rotation around the Z axis. There are also three degrees of translation, which is a change in both direction and distance, along the three axes. While a total of six degrees of movement through space is possible, most species are unable to perform all six.

Normal position refers to the usual stance an organism adopts in relation to specific reference stimuli, typically gravity, light, and its relation to the substrate (Schöne, 1984; Waterman, 1989). Normal positions differ among species, although the usual is for the dorsal side to be on top. For an organism to engage in locomotion, generally the animal must be in its normal position. Most sensory perception organs are located so that they function properly only when an organism becomes displaced into an abnormal position, it will instinctively attempt to return to its normal position, a behavior called the "righting reflex" (Waterman, 1989).

The equilibrium position, or balance, is a special state of normal position. It affects the ability of organisms, especially long-legged terrestrial animals, to resist gravity and allow them to remain upright. Organisms that utilize the equilibrium position have specialized internal mechanisms, or gravity receptors, which can detect slight variations in the gravitational force and adjust their bodies accordingly.

The resting position places the organism in a position that provides the most comfort. In this position the organism is not in motion and this position provides the least resistance to gravity.

Stabilizing orientation is a method of orientation that allows an organism to align itself to environment (Schöne, 1984). The stabilizing systems work whether the organism is at rest or in motion and they allow the animal to maintain or specifically alter their movements. Many species use visual mechanisms to stabilize their orientation in space. The dorsal light reaction keeps organisms, especially fliers and aquatic species, in the correct orientation by responding to the distribution of light and dark in the environment (Waterman, 1984). By positioning themselves so that the dorsal side is toward the light, the organism is able to hold its normal position. Organisms can also use the horizon, along with vertical and horizontal edges, to align themselves with their surroundings. Using optokinetic responses is another method that allows orientation to be maintained. If the surroundings of an animal are rotated, it will follow the movement with its visual field. This optomotor response "is a corrective movement produced by an orientation mechanism that stabilizes and actively controls an animal's position, or change of position, relative to its surroundings" (Schöne, 1984, p. 15).

Gravitational and inertial sensors, or statocysts, are other methods that allow organisms to remain aligned in space (Waterman, 1989). Statocysts can detect the downward pull of the earth providing a basic reference for the vertical and horizontal alignment of the organism. They are commonly fluid filled vesicles lined with sensory cilia and statolith, which are small grain-like bones. These bones are shifted by the gravitational force and their movement tilts the cilia in the direction of the gravitational pull. The direction of the cilia provides the nervous system with information as to the orientation of the animal. Gravitational statocysts are generally paired right to left on the head region of the organism and are found in a majority of all species except insects.

Statocysts also provide the organism with information on changes in linear or angular velocity, or inertia. Just as the statoliths displace the cilia due to gravity, they also cause the cilia to bend when an external force acts on the animal's speed of movement. The animal is able to distinguish between gravitational and inertial movement of the cilia as inertia only displaces the cilia if the animal is changing the velocity of its movements.

Goal-directed orientation permits an organism to reach a predetermined destination located either near, referred to as proximal orientation, or far, termed distal orientation (Schöne, 1984). The goals for proximal orientation can normally be directly perceived by the senses and the cues for navigation emanate from the goal itself. Proximal orientation includes target orientation where a single brief movement brings the organism to the goal. Behaviors such as hunting/attack, feeding and sexual interactions are all target orientations. Target orientation requires precise evaluation of the goal's distance and direction.

For goals that must be obtained using distal orientation, mechanisms that are not directly related to the goal are required (Schöne, 1984; Waterman, 1989). When the goal cannot be detected by the organism, methods that allow for the use of intermediate cues must be used to indicate the direction, distanshould be well d the goal. These mechanisms may include compass orientation, a spatial reference in relation to a directional orientation; vector orientation, which takes into account both direction and distance; or course orientation, which represents distance only. Distal orientation can be used to locate a narrowly defined location, such as a specific foraging area or mate, or involve a more general goal as in a wintering location for a migrating species. Distal orientation entails three areas of navigation interest: (a) how the organism determines what direction it will take, (b) how the direction is maintained, and (c) how the goal is recognized (Schöne, 1984).

While there is no clear answer as to how an animal chooses a particular bearing, for any goal directed orientation to take place certain conditions must be met. First the organism must be ready, or motivated to orient (Schöne, 1984). The organism must have an internal need that will compel it to reposition itself. These drives may include hunger, thirst, need for protection or procreation. There must also be external factors, such as releasing and directing stimuli, which propel the animal into action when the correct internal conditions exist. The releasing and directing stimuli cause an organism to respond to particular cues with certain innate behaviors. When an animal runs to escape from capture, the sight, sound or smell of the hunter is the releasing stimulus for the animal to bolt and the cover the animal dashes for is the directing stimulus. Lastly, the organism must be able to perceive the stimuli and have the correct sensory receptors to detect the different elements of orientation. The organism needs to be able to decide whether all of its body, or only part, needs to be oriented. The organism also needs to be able to use information about the spatial reference values in its environment.

Reference stimuli provide an organism with information as to the correct bearing of goals in their environment, however, they do not ensure that the animal will reach its goal (Schöne, 1984). Reference stimuli can be classified by their distribution in space and can be broken down as follows:

1. Fields of parallel stimuli (usually of uniform intensity)
2. Fields of graded intensity (gradients)
3. Fixed points (landmarks)
4. Trails (Schöne, 1984, p. 32)

Fields of parallel stimuli provide an organism with a constant spatial reference no matter where the animal is. Examples are the sun, the magnetic field and gravity. They maintain the same direction regardless of where or how the animal is positioned. Fields of parallel stimuli can be used by organisms as points of reference to maintain a compass course. One such compass involves the use of celestial cues (Waterman, 1989). The sun, moon, and stars all provide an organism with reference points that allow for long distance navigation. While the sun appears to be the most commonly used of these celestial compasses, nocturnal animals could quite possibly orient using the moon and stars, though, little research has been done in this area. Studies done with migratory birds (Able, 1983, 1984; Emlen, 1975; Wiltschko, Daum, Fergenbauer-Kimmel & Wiltschko, 1987a) have also shown that some species of birds can detect the correct migratory direction using stellar information. Sun compass orientation was first discovered by von Frisch (1948) while studying the behavior of bees. He found that bees could locate saucers of sugar water placed in sites that had no discernible landmarks. This ability was affected, however, if the bees were detained several hours at their hives before they were allowed to return to the site. Von Frisch found that when detained, the bees would miscalculate the location of the sugar water in a clockwise angle that closely reflected the bearing of the sun. These findings indicated to von Frisch that not only could the bees use the sun to navigate, but they were also able to time-compensate for the sun's daily changes. The relevant information provided by the sun for navigational purposes appears to be the azimuth, or horizontal component of movement (Able, 1991; Schöne, 1984; Waterman, 1989). Research using clock shift experiments have illustrated this (Waterman, 1989). Animals that have had their internal sense of time manipulated using artificial day and night cycles miscalculate their orientation to a goal with the angle of error corresponding to the time difference between natural daylight and the experimental condition. Such inaccuracies indicate that animals that use the sun for navigational purposes are able to compensate for the horizontal movement of the sun (Waterman, 1989). Although the use of the sun compass to guide long-distant travel has been primarily researched using bees (von Frisch, 1967) and species of birds (Able, 1991; Akesson & Sandberg, 1994; Lushi & Dall'Antonia, 1993; New Scientist, 1989; Sandberg, 1991), other species, such as the marine isopod Idotea baltica (Ugolini & Pezzani, 1993), the digger wasp (Schöne & Tengo, 1991), and the sand fiddler crab (Cameron & Forward, 1993) have also been shown to utilize a sun compass.

Sky polarization is an extension of the sun that provides an organism with reference for navigation (Schöne, 1984; Waterman, 1989). The oscillation of electromagnetic waves perpendicular to the direction that light travels forms polarized planes, or e-vector. The e-vector is arranged in latitudes that extend from the sun at one pole to the antisun at the other. Migrating birds appear to use polarized light to help them detect the azimuth and to orient (Akesson & Sandberg, 1994; Moore & Phillips, 1988; Sandberg, 1991).

The geomagnetic field is another source of parallel stimuli that allows for a compass course to be maintained (Able, 1991; Schöne, 1984; Waterman, 1989). The earth has two magnetic poles, north and south, that create strong magnetic lines of force with an upward pull from the south pole and a downward pull from the north. At the equator, the pull is horizontal in relation to the earth's surface. These three directional forces produce a magnetic field with both horizontal and vertical components. The magnetic field also varies in its intensity where there is a drift between the magnetic poles and the geographic rotational poles (Waterman, 1989). The vertical and horizontal components and the intensity of the magnetic field can be used by organisms as a type of compass. Studies using migratory birds have demonstration that they are able to use such magnetic cues (Able & Able, 1990; Munro & Wiltschko, 1993; Wiltschko & Wiltschko, 1992) and other species, including honey bees (Collett & Baron, 1994), newts and loggerhead sea turtle hatchlings (Lohmann, 1993), have also been found to use magnetic compass orientation.

Gradients allow an organism to detect its direction of travel by gaging the strength of the stimuli in relation to the goal (Schöne, 1984; Waterman, 1989). As the organism nears the goal, the intensity of the stimuli increases. The gradient can be either radically symmetric, with concentric rings of equal intensity, or distributed along a moving medium, like air, into an extended plume. Gradients include such stimuli as odor, thermal properties, salinity, light and moisture.

Although it appears to be random movement, kinesis is one type of orientation to a stimulus gradient (Domjan & Burkhard, 1993; Schöne, 1984; Waterman, 1989). Different levels of a gradient elicit different locomotive responses from an organism. When an organism is removed from its optimal level of a gradient, its random movement increases thus improving the odds that the animal will return to its proper environment. When the organism reaches its preferred level of the stimulus its movements decrease and eventually stop.

Chemoreceptive direction finding is another form of gradient orientation (Benhamou, 1989; Waterman, 1998), although odors can also serve as trails and landmarks. Pigeons have been found to use odor gradients to locate their lofts (Benvenuti & Brown, 1989; Iole, Nozzolini & Papi, 1989; Papi, Gagliardo, Fiaschi & Dall'Antonia, 1989; Wallraff, 1993). Pigeons permitted to have free access to odors and wind currents around their lofts were much more accurate in locating their way home than birds denied access or rendered anosmic.

Landmarks are fixed, distinctive features in the environment that provide references to a goal (Schöne, 1984; Waterman, 1989). They supply the animal with information about the distance and direction to the goal. They can be both proximal or distal and are not limited to their size or shape. Landmarks can be used by an organism for piloting within its home range or for navigating long distances. By learning the features of their environment the organism can determine its location and the direction and distance needed to reach a particular goal. Goldfish (Warburton, 1990), the digger wasp (Schöne & Tengo, 1991), pigeons (Cheng, 1989) and honey bees (Gould, 1990) were all found to use local landmark cues to detect important nesting or foraging areas in their habitats. Distal landmarks, such as large geographic features are possibly used by migratory birds for locating their destinations, although there is no firm evidence to support this theory (Ehrlich, Dobkin & Whyeye, 1988). Distal landmark cues also have been suggested to be important tools for establishing the boundaries of home ranges and the territories of conspecifics by rats (Margules & Gallistel, 1988) and hamsters (Etienne, Lambert, Reverdin, & Teroni, 1993) in.

Although landmarks are often visual, they can also be chemosensory (Able, 1991; MacKintosh, 1973; Schöne, 1984; Waterman, 1989). When odors are used as landmarks and trails, they are an important means for animals to spatially orient to their surroundings. Grassman (1993) found implications that sea turtles may use chemical imprinting to help them home to their nesting sites. Mice use odors (MacKintosh, 1973) to help establish the boundaries of their territories. Tomlinson and Johnston (1991) found that hamsters also use odors to develop spatial relationships in their environment.

Trails are an extension of landmarks or a series of fixed points that often convey specific information about its markers (Schöne, 1984). Odor trails can be either a discrete row of scent, as in a scent marked boundary, or a continuous band. Rattlesnakes have been shown to follow post-strike prey by using odor trails (Chizar, Smith, & Hoge, 1982; Furry, Swain, & Chizar, 1991) and research using ants (Harrison, Fewell, Stiller, & Breed, 1989) has also indicated that odor trails are important for locating foraging areas and nests.

Although the different reference stimuli are individually important, it is unlikely that any species uses only one type of reference cue to spatially orient themselves (Able, 1991). Research looking at spatial abilities has found that animals often employ a primary cue that has precedence over other cues (Able, 1991; Cheng, 1989; Lushi & Dall'Antonia, 1993; Schöne, 1984; Schöne & Tengo, 1991), however, when the primary cue is not accessible the animal is still capable of using other cues to orient themselves. This is an important adaptation, especially for long distant migrants that rely on an inconstant primary cue, such as sun compass orientation. On cloudy days, these migrants would need to depend on other cues, such as landmarks, to maintain their course.

The ability to use multiple reference cues would be just as invaluable, however, to an animal that must navigate only a relatively short distance from one known site to another within its home range or territory or explore new locations for forage and mates (Schöne, 1984, Waterman, 1989). Studies have indicated that many species use multiple orientation mechanisms and cues for goal directed movements, including hamsters (Etienne, Lambert, Reverdin, & Teroni, 1993), honey bees (Gould, 1990), digger wasps (Schöne & Tengo, 1991) and pigeons (Luschi & Dall'Antonia, 1993). The use of multiple cues allows an organism to orient in many different environmental conditions. MacKintosh (1973) found that although house mice have a preference for visual cues when available, they are primarily nocturnal in their foraging and often navigate using odor cues.

Path integration, or dead reckoning, is another navigational strategy were orientation information is produced by the animal itself, or idiothetic (Benhamou, Sauvé, & Bovet; Etienne, Maurer, & Saucy, 1988; Etienne et al., 1993; Etienne, Maurer, & Séguinot, 1996; Gallistel & Cramer, 1996; Schöne, 1984). As an animal moves about its environment its location in relation to a fixed point of reference, such as a nest, is continuously updated by internal processes that compute the angles and linear signals generated by the animal's movements. Path integration allows an animal to "home", or return to its starting point, without relying on external cues. This sort of navigation would be an important tool for central foragers that must journey out to find food and then return to a nest or burrow. Dead reckoning would also be an beneficial strategy for animals that must forage in novel environs where external spatial cues have not been established (Etienne et al., 1996). Path integration is most effective, however, for short distances. When animals must travel farther, path integration used alone results in errors in direction and distance estimates. Instead, animals most likely incorporate the use of landmarks to augment the performance dead reckoning.

Little research has been done on the orientational behavior of the desert tortoise. Research done with other species of chelonian suggests, however, that some turtles and tortoises are able to maintain directional courses (Gould, 1959; Lemkau, 1970; Tinklepaugh, 1932). The ornate box turtle (Terrapene ornata ornata agassiz) (Metcalf, 1978) showed a varied proficiency of homing among subjects, with the ability appearing to break down after 3.2 km. Research by Emlen (1969) found that the painted turtle, (Chrysemys picta marginata), appeared to use local topographical landmarks, but not celestial or gravitational cues, to return to their home ponds. In contrast, DeRosa and Taylor (1980) concluded that the painted turtle, along with the spiny softshell turtle (Trionyx spinifer) and the eastern box turtle (Terrapene carolina) could use both celestial cues and geotatic orientation. In a study by Gibbons and Smith (1968) there was evidence that the gopher tortoise (Gopherus polyphemus) used a sun compass for orienting. Gourley (1974) also found that the gopher tortoise used the sun-compass, however, but theorized that landmarks would be the preferred cue for orientation when available.

The gopher tortoise belongs to the same genus (Gopherus) as the desert tortoise. Observations of the desert tortoise have provided examples of behavior that suggest that, like the gopher tortoise, the desert tortoise uses multiple navigational cues. This would feasiblely facilitate the tortoises' existence in its environment. The desert tortoise lives in the arid regions of the Western United States and Northwestern Mexico, from the south west tip of Utah to the Sonoran Desert and from Pima County, Arizona to the Mojave Desert in California (Stebbins, 1985). The small amount of rainfall per year provides only a few months of sparse forage and little available water for the animals that inhabit these areas. These deserts also experience extreme seasonal temperature differences, with the summer months exceeding 38°C and then dropping below freezing in the winter in some of the higher elevations of the Mojave and Great Basin deserts. Consequently, the animals and plants that reside in these regions must have adaptations that permit survival in such severe conditions.

The desert tortoise has evolved both physiologically and behaviorally to allow it to exist successfully in its habitat. The specialized physiology of the tortoise maximizes its use of obtainable resources and provides protection for the animal (Woodbury & Hardy, 1948). The carapace and plastron are formed by bones covered with horny plates, or scutes, with the head and limbs protruding from openings in the shell to allow the animal movement. When the animal is disturbed, however, the legs and head are retracted into the shell creating a continuous barrier to protect the internal organs from predation. The shell is also waterproofed by keratin, thus reducing the amount of moisture lost through metabolism and breathing. This becomes crucial during the extremely high temperatures of summer when little moisture is found through rainfall or green vegetation.

The internal systems of the tortoise are another physiological adaptation that permits the tortoise to survive in the desert. The long intestine is arranged in folds that allows for slower digestion so that optimum amounts of nutrients can be obtained from the animals' high cellulose diet (Dean-Bradley, Tracey, Castle, & Esque, 1995; Spangenberg, 1995). This flexible digestive system enables the tortoises to establish sufficient lipid stores for annual hibernation and possibly for extended periods, sometimes over several years, when lack of seasonal rainfall prevents the growth of spring annuals, a major food source for the tortoise (K. H. Berry, personal communication, February 10, 1994). During these intervals, the search for forage would expend more energy than could be replaced by the available resources.

The bladder of the tortoise has also been modified by evolution to accommodate desert survival. Its large size is capable of storing substantial amounts of water. While the walls of the bladder are highly permeable to water for reabsorption, the water stored in the bladder is also a means for holding uric acid, the urinary waste of the tortoise (Ernst, Barbour & Lovich, 1994; Grover & DeFalco, 1995). Uric acid is insoluble in water, allowing for large quantities of the solids to accumulate before they need to be excreted. This results in reduced moisture expenditure as it reduces water lost through the elimination of urinary waste products.

These physiological changes alone are not enough to ensure the survival of the tortoise. While cold-blooded species do not require as much caloric input as warm-blooded animals to exist, the effect of the tortoises' ectothermic metabolism means that their foraging and mating are limited to optimal temperature conditions (Woodbury & Hardy, 1948). Combined with limited available resources, the tortoise must have behavioral adaptations to inhabit such an inhospitable environment. Studies on the behavior of the desert tortoise have found that the tortoise employs strategies that optimize the use of its habitat (Berry, 1974, 1986; Grover & DeFalco, 1995; Hansen, Johnson & Van Devender, 1976; Jennings, 1993; Sazaki & Boarman, 1994; Woodbury & Hardy, 1948). The desert tortoise resides in semi-isolated populations with possible complex social structures (Berry, 1974). Each animal occupies a home range that can reach in size to 76.9 ha for the males, although Berry (1986) suggests that these estimates may be low. These areas overlap with other tortoises' and both males and females appear to aggregate for basking and hibernation. Within these activity areas the tortoise appears to be aware of the location of choice foraging (Jennings, 1993), drinking sites, mates (Berry, 1974; Grover & DeFalco, 1995), and protection (Berry, 1974, 1986; Woodbury & Hardy, 1948). Desert tortoises have been tracked moving from one of these sites to another in straight-line distances (Berry, 1972; Grover & DeFalco, 1995) indicating they possess a spatial awareness of their home ranges.

Woodbury and Hardy (1948) observed that the tortoise appears to have both daily and seasonal cycles of movement that yield the greatest degree of temperature comfort, nourishment, and moisture. Tortoises emerge from their permanent winter dens after hibernation in March and April when the ground temperatures reach the normal activity range for the animals (26 - 29 °F). It is also during this period that the spring annuals are the most abundant. Upon emergence, Jennings (1993) noted that for the first several months the desert tortoise remains nomadic in its movements. The animals rarely remained more than one night in any particular summer burrow and often used non-burrow shelter. These random wanderings ceased in May when the availability of fresh forage decreased. The tortoises then began to travel less frequently in a non-random fashion making use of old and new burrows adjacent to valuable forage sites. It was observed that the desert tortoise was a very selective forager and that the animals were able to find preferred plants effectively (Jennings, 1993; Spangenberg, 1994). During this time the temperatures were also increasing and ready access to burrows was essential to provide protection from heat and moisture loss. As the available forage declined further in June, the movement of the tortoises also diminished. Jennings found that animals preferred the use of a single burrow or den close to remaining accessible forage and travel was restricted to morning and evening visits to feeding sites.

The desert tortoises foraging movements suggest that they possess a spatial understanding of their environment and that they use spatial reference cues to navigate successfully within it. The tortoises' random movements early in the season bring them to adequate foraging areas and other resources that are returned to later in the season. A potential explanation for these excursions is that the tortoise is establishing a system of local landmarks to direct the animal to choice feeding, basking and drinking sites.

Other behaviors also give evidence that the desert tortoise is capable of spatial orientation. Tortoises have been detected using trails to travel from one site to another (Berry, 1986), especially along washes and washlets (Jennings, 1993). Odor also appears to play an important role in the tortoises' use of their habitat. Tortoises seem to use urine as a means of burrow identification (Berry, 1986; Nichols, 1957) and Berry (1986) postulated that the desert tortoise uses chemical signals produced by subdentary glands and the cloaca in the trailing and sexual recognition of mates. The use of odors by tortoises is suggested by the observation that the animals engage in frequent "sniffing" behavior as they travel (Berry, 1974, 1986; Grover & DeFalco, 1995).

In another study examining the behavior of relocated desert tortoises, Berry (1974) found that transplanted tortoises tended to orient home in a straight-line direction. In addition, tortoises tracked using radio transmitters have also been found to travel long straight-line distances within and outside the home ranges (Berry, 1986; Sazaki & Boarman, 1994). Berry (1974, 1986) suggests that these straight-line movements indicate that the desert tortoise is capable of compass orientation.

Ascertaining what orientation cues are being utilized by the desert tortoise could have important consequences on the survival of the desert tortoise. Determining such cues could assist in establishing suitable CH, by ensuring that such habitats contain the necessary landmarks, trails, etc. for finding needed resources. Knowing what spatial reference cues are involved in how the desert tortoise orients to its environment could also help to designate suitable relocation sites, a wildlife management strategy that may be crucial for saving the desert tortoise as human populations encroach on tortoise habitats.

Although the knowledge concerning spatial orientation has the potential of proving significant, this researcher could find no studies that examined the use of spatial reference cues by the desert tortoise under controlled conditions. While naturalistic observations are important for identifying certain behaviors, they are not sufficient for determining the cause of the behavior. Many separate or combinations of variables could be generating a behavior as the effects of extraneous variables cannot be accounted for. Although studies of chelonian orientation (discussed earlier in this paper) have indicated that turtles and tortoises use landmarks and compass orientation, the results are conceivably confounded. These studies were conducted outside which increases the difficulty of controlling for extraneous variables. Animals that seemed to be following a compass direction could have been responding to an odor plume or large distal landmarks. Variables such as different capture sites, the adequacy of the distance from release site to goal, the location and time spent in holding pens and the likelihood of conflicting or multiple cues were not addressed.

This study addressed the question of spatial reference cue use by the desert tortoise in a controlled condition. Three reference cues were manipulated: an odor, a landmark and a light. Experiment 1 investigated the possible use of these cues for running a maze to obtain a reward of food. Subjects were required to run a maze with the three cues presented one at a time. The tortoises' use of each cue as a means of locating the goalbox that contains the reward was examined. The subjects' acquisition rate for each of the three conditions was analyzed for significant differences among the percentage of correct goalbox choices (CGC) using the cues. It was hypothesized that the desert tortoise would be sufficiently able to navigate the maze employing each of the three cues. It was also postulated, however, that a significant difference would be found among percentage rates for the individually presented cues, giving evidence the desert tortoise uses cue preferences for orientation, with a bias for using landmark cues while traveling within their environs.

Experiment 2 further investigated possible cue preferences and the use of a primary cue by the desert tortoise. The subjects were tested in a discrimination task where all three cues were presented simultaneously. If the subjects were using a primary cue strategy, a preference for one cue should emerge. It was proposed that the desert tortoise does use a primary cue strategy and that the subjects will demonstrate a preference for the landmark cue while navigating the maze.

## EXPERIMENT 1

### Method

#### Subjects

At the start of the study the subjects consisted of 16 captive bred juvenile desert tortoises. Four of the subjects were dropped from the study, as two subjects refused to traverse the maze and two animals died. The size of the subjects ranged from 40 to 440 g with carapace lengths of 50 mm to 150 mm. At this size the sex of the tortoises was not possible to determine. The subjects' ages at the start of the study were five at 5 months, five at 1 year and six at 3 years old. The 5-month-olds and 1-year-olds were housed in pairs in plastic containers measuring 37 x 47 x 13 cm high while the five larger animals were held in a 61 x 92 x 36 cm high plastic container. All of the containers were placed on shelving in a room heated to 24 °C. The subjects were housed with siblings to help prevent the transmission of possible diseases and parasites. The temperature surrounding the containers was kept at 29 - 35 °C using heaters and incandescent lights. A full-spectrum UV light source placed approximately 35 cm above the containers was provided on a 12 hr rotating light/dark schedule. The containers were lined with a layer of newspaper covered by paper towels that were changed as needed. The subjects were fed a diet of assorted leafy green vegetables once daily after all experimental trials were completed. Calcium carbonate powder was sprinkled on the food weekly. Fresh water was made available to the subjects for drinking and soaking in the mornings and after feeding. Liquid vitamins were added to the water weekly.

### Materials

Apparatus. The maze was made of particle board that was painted gray and coated with polyurethane. The overall dimensions of the apparatus are diagramed in Figure 1. The startbox was located at the front of the maze and had a separate door and lid that measured 20 x 20 cm and could be removed and replaced by the experimenter. Except for the back wall (see Figure 1), all of the goalbox and maze walls were 20 cm in height. When not in use, the holes located in the back wall were covered by pieces of grey cardboard measuring 15 x 8 cm wide. Each goalbox contained a round indented food cup measuring 1 cm in diameter that was painted light grey and placed 2.5 cm from the back wall. The food cups were centered between the goalbox sides. A black line placed 10 cm from the back wall was used to indicate a goalbox choice. A row of brown dots leading into each goalbox was painted onto the floor of the apparatus for placement of the odor cue. This was to control for any visual cues derived from the odor cue solution from being utilized.

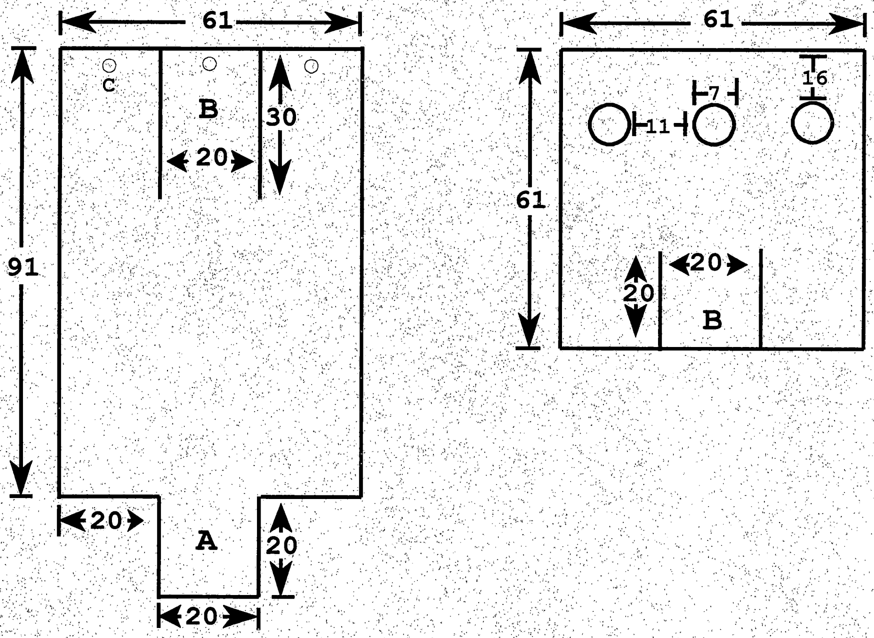

Figure 1. Floor plan of the apparatus (left) and back wall dimensions (right). A = Startbox. B = goalboxes. C = food cups. All measurements are in centimeters.

The experimenter sat on a stool behind the startbox with the maze placed on a table (61 x 46 x 84 cm high) in a closed 2.5 x 3.0 x 2.7 m high room. The walls were covered by black plastic hung from the ceiling. The floor of the room was grey linoleum and the lighting consisted of a fluorescent ceiling fixture. The apparatus was placed under this light fixture. The room's temperature was kept at 26°C during the trials.

Spatial reference cues. The light cue consisted of a 61 cm long, 20 watt fluorescent full-spectrum UV light bulb (Ott-lite Plant Growth Tube, OT2012P) placed in a standard under-cabinet fluorescent light fixture used without the light diffuser. The fixture was mounted to the outside of the back wall with velcro so that the light bar was centered over the goalbox hole. The visual landmark was a wood block (4 x 4 x 10 cm high) painted white and placed adjacent to the right wall at the entrance of the goalbox. The odor cue consisted of drops of alcohol-free vanilla flavoring placed in the center of each brown dot leading into the goalbox. The vanilla was pretested to confirm that the odor was discernable by the subjects.

Procedure

Pretraining. All of the subjects were pretrained to learn to travel from the startbox to the goalboxes by making food available to the subjects when they reached the food cups located in each goalbox. At the outset of a trial the animal was placed in the startbox with the door and lid in place. A food reward consisting of a small piece of romaine heart was placed into each food cup. After approximately 30 s the startbox door and lid were removed by the experimenter. The animal was allowed to move freely within the apparatus until it entered a goalbox and obtain the reward. After the subject had eaten the reward it was placed back into the startbox, the entire maze was cleaned with a mild disinfectant soap solution to remove any odors, and the next trial was begun. If the animal did not leave the startbox after 5 min the animal was removed and then replaced into the startbox. This was counted as a no-trial and a new trial was started after 30 s. For subjects that continually refused to leave the startbox, or if they left the startbox but did not move toward any goalbox, a shaping procedure was employed. This consisted of placing small pieces of food leading toward the goalboxes. For each subsequent trial the first piece of food was placed farther from the startbox until the subject needed to travel the length of the maze to obtain the first piece of reward. This shaping procedure continued until the animal consistently entered the goalboxes. To prevent positional habits, a goalbox was blocked from entry if it was visited by an animal more than two times consecutively. The subjects were run for 6 trials per day and the order in which they were run was randomly selected. Pretraining continued until each animal visited each goalbox once daily for two consecutive trial days. Animals that were not able to meet this criterion after ten days of pretraining were eliminated from the study.

_Training_. The training trials started the day after the subjects met the criteria for the pretraining trials. The subjects were divided into three groups and each group was assigned to one of the three spatial cues. The procedure for Experiment 1 was the same as for the pretraining trials except that the food reward was only available in the goalbox marked by the assigned cue. On all days, each goalbox was designated as containing the reward for two trials with the order counterbalanced. A subject was considered to have made a correct goalbox choice (CGC) when it passed the line at the end of the goalbox. An animal refusing to leave the startbox after 3 min, or enter a goalbox after 5 min, constituted a no-trial and the subject was lifted and replaced into the startbox. The cue and food reward were then set up in the next goalbox location, the entire maze was cleaned and a new trial begun. For each cue, the subjects were trained for six trials per day until they each reached a criterion of 85% correct responses for two consecutive days or underwent sixty trial days. When the criterion was fulfilled using one cue, the subject was assigned to one of the remaining cue conditions until each animal had reached criteria using all three cues presented in three separate learning sets. The new learning sets started on the third day after the end of the last set, and the order in which a cue was assigned to a subject was counterbalanced.

## Results

The data were prepared for analysis by dividing each learning set (LS) into 12 five-day increments. The percentage of correct responses for each increment was calculated for each subject and then analyzed using a 3 x 12 (Cue x Increment) mixed ANOVA with repeated measures(an alpha level of .05 was used for all statistical tests). As seen in Table 1, no significant difference was found between the cue groups nor was there a significant interaction. Significance was shown, though, for the increments main effect. An examination of the within-subject contrasts of the increment means finds a significant increase in the percentage of CGC from Increment 1 ($M = .34$, $SD = .115$ ) to Increment 11 ($M = .41$, $SD = .119$), $F(1, 33) = 7.21$, $p = .01$. However, due to a slight decline in the percent correct for Increment 12 ($M = .40$, $SD = .151$) the increase of CGC from Increment 1 to Increment 12, was only marginally significant, $F(1, 33) = 3.70$, $p = .06$.

Table 1

Analysis of Variance for Correct Goalbox Choice Across Increments

| | | F |
|---|---|---|
| Source | df | CGC |
| | Between subjects | |
| Cue (C) | 2 | 2.24 |
| Error | 33 | (.003) |
| | Within subjects | |
| Increments (I) | 11 | 2.84** |
| I x C | 22 | 1.48 |
| Error | 363 | (.01) |

Note. Values in parenthesis represent mean square errors. CGC = correct goalbox choice.

*$p < .05$. **$p < .01$.

When the cues were analyzed individually using a one-way ANOVA (see Table 2), significance was found for the light and landmark cue increments, but not for the odor cue. In Figure 2 an increase in the CGC means from Increment 1 to Increment 12 can be seen for the landmark and light cue, while the odor cue means show a small decline. However, an inspection of the within-subject contrasts for the three cues shows that there was no significant change between Increment 1 and 12 for either the landmark, light, or odor cues, $Fs(1, 11) = 3.66$, 1.48 and .40, respectively, $p > .05$.

Table 2

Analysis of Variance for Correct Goalbox Choice Across Increments for Individual Cues

|  |  | F |
|---|---|---|
|  |  | CGC |
| Source | df | Landmark |
| Within subjects |  |  |
| Increments | 11 | 2.28** |
| Error | 121 | (.01) |
|  |  | Light |
| Increments | 11 | 2.20* |
| Error | 121 | (.01) |
|  |  | Odor |
| Increments | 11 | 1.21 |
| Error | 121 | (.009) |

Note. Values in parenthesis represent mean square errors. CGC = correct goalbox choice.

*$p < .05$. **$p < .01$.

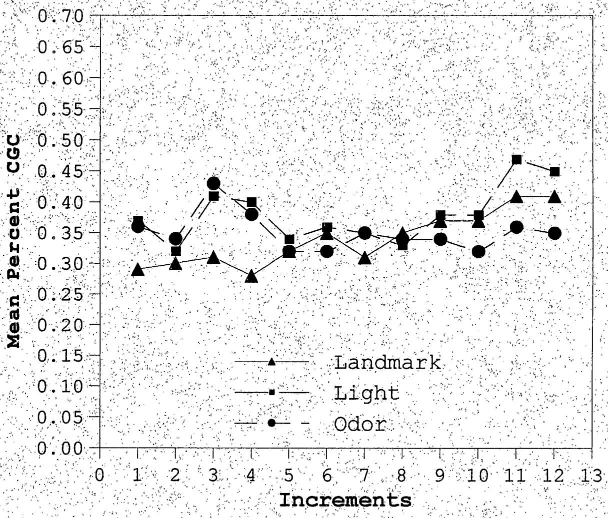

Figure 2. Mean percent of correct goalbox choices for individual cues across 12 five-day increments.

The means graphed in Figure 2 also show an erratic pattern of CGC among the increment means. This inconsistent pattern could possibly be due to the subjects being trained on the landmark, light and odor cues in three subsequent LSs. It is possible that the subjects experienced interference from LS 1 in their attempts to use the next cues in LSs 2 and 3. This was investigated by comparing the LSs with a 3 x 12 (Learning Set x Increments) mixed ANOVA with repeated measures. Although a significant main effect for the LSs was not found, F(2, 33) = 1.683, p = .20, there was a strong interaction between the three LSs and increments, *F*(22, 363) = 4.602, *p* < .001. A Tukey *a* post hoc analysis shows that by Increment 12, LS 1 had a significantly higher mean percent of CGC (*M* = .51, *SD* = .166) than either LS 2 (*M* =.36, *SD* = .132) or LS 3(*M* = .35, *SD* = .106). Analysis of the individual cues also finds a significant interaction between the LSs and increments, indicating that the LS in which the landmark, light and odor cues were learned did have an effect on the CGC, *F*s(22, 99) = 2.49, 2.40 and 1.66, respectively, *p* < .05.

As possible interference in CGC was inferred by the comparison of the LSs, the same ANOVA analysis was rerun using only the data from LS 1. The results shown in Table 3 indicate that, like the results from the analysis using all LSs, there was no significance found between the cue means or a significant interaction. The means for the light, landmark, and odor cue were (standard deviations are in parentheses) .61 (.154), .54 (.135) and .31 (.017) in order, with the light cue mean significantly higher than the odor cue. Also, consistent with the outcome from the first analysis using all learning sets, results from the data of LS 1 indicate that there was a significant main effect for the increment means. Unlike the first analysis, however, in LS 1 there was also a significant increase in CGC between Increment 1 (*M* = .31, *SD* = .123) and Increment 12 (*M* = .51, *SD* = .166), *F*(1, 9) = 8.31, *p* = .02.

Table 3

*Analysis of Variance for Correct Goalbox Choice Across Increments, Learning Set 1 Data Only*

|  |  | *F* |
|---|---|---|
| Source | *df* | CGC |
| Between subjects |  |  |
| Cue (C) | 2 | 1.00 |
| Error | 9 | (.002) |
| Within subjects |  |  |
| Increments (I) | 11 | 4.71** |
| I x C | 22 | 1.28 |
| Error | 363 | (.01) |

*Note*. Values in parenthesis represent mean square errors. CGC = correct goalbox choice.

**p* < .05. ***p* < .01.

When a one-way ANOVA was run for each cue using only the LS 1 data, significant increment main effects were found for the light and landmark cue, but not the odor cue (see Table 4). When the increment means, plotted in Figure 3, are examined, an increase in CGC for the landmark and light cues is evident, but without the fluctuation seen in Figure 2. The odor cue means, however, continue to show a variable pattern and a within-subjects contrast showed that the CGC means significantly declined from Increment 1 to Increment 12, F(1, 2) = 27.43, p = .04. Surprisingly, while the landmark cue showed the steadiest rate of increase in CGC between the first and last increments, the within-subject contrasts only found the light cue as having a significant increase from Increment 1 to Increment 12, F(1, 3) = 11.14, p = .04.

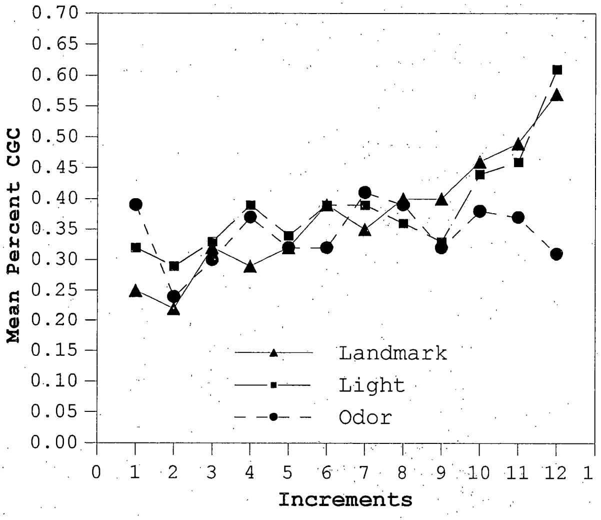

Figure 3. Mean percent of correct goalbox choices for individual cues across 12 five-day increments, Learning Set 1 data only.

Table 4

*Analysis of Variance for Correct Goalbox Choice Across Increments for Individual Cues, Learning Set 1 Data Only*

| | | *F* |
|---|---|---|
| | | CGC |
| Source | *df* | Landmark |
| | Within subjects | |
| Increments | 11 | 4.72** |
| Error | 44 | (.01) |
| | | Light |
| Increments | 11 | 2.90** |
| Error | 33 | (.01) |
| | | Odor |
| Increments | 11 | 0.78 |
| Error | 22 | (.01) |

*Note*. Values in parenthesis represent mean square errors. CGC = correct goalbox choice.

*$p$ < .05. **$p$ < .01.

Although not originally planned for in the experimental design, the potential of an age difference in cue use was also investigated using a 3 x 3 x 12 (Cue x Age x Increments)mixed ANOVA with repeated measures. The analysis was run using the data from all the LSs, as LS 1 did not have all age groups represented in all cue groups due to the loss of subjects. The results of the analysis do not show any significant results for any of the main effects or interactions.

Also of interest was the potential use of a goalbox position preference. It was possible that the subjects were selecting a goalbox because of its location in the maze, not because of the cue designating the reward. The percentage of times a subject chose either the right, left, or middle goalbox out of the total number of trials for that subject was calculated for each LS and the resulting data was analyzed using a 3 x 3 (Cue x Goalbox Position) mixed ANOVA with repeated measures. Only LS 1 showed a significant goalbox position main effect, $\underline{F}(2, 22) = 5.279$, $\underline{p} = .02$. When the means were compared with a within-subjects contrast (see Figure 4), a significant variation was found between the middle box and both the right and the left goalboxes, $\underline{F}s(1, 11) = 6.186$ and 38.20, $p < .01$, respectively, but not between the right and left goalbox positions. No significance was found for the cue main effect or for an interaction between the cues and the goalbox positions for any of the LSs.

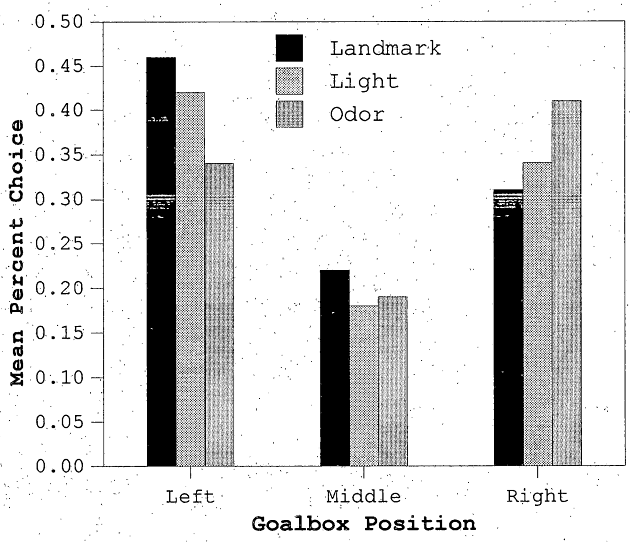

Figure 4. Mean percent choice of goalbox position by cue.

## Discussion

In the first analysis, that included the data from the combined cues and all LSs, the results indicate that by Increment 11 the animals were able to determine the goalbox that contained the reward, though their performance declined in Increment 12. Although assessment of the composite learning sets CGC means provides indications that the subject were associating the cues with the reward, an evaluation of the individual cue CGC means reveals that use of the separate cues was inconsistent. These findings not only generate some doubt as to whether the subjects were actually using the cues to locate the reward, but they also conflict with the hypothesis that the subjects would be capable of navigating the maze using all three of the spatial cues.

Comparing the subjects' CGC in the different LSs, however, yielded some insight as to the conflicting findings from analyses using all LSs. By Increment 12, the subjects' combined LS performance for correctly choosing the goalbox paired with the reward was dramatically lower in LSs 2 and 3 than in LS 1. When the cues were assessed singly, the means were also lower in LSs 2 and 3 for the light and the landmark cues. While Seidman (1948) found indications that sliders (Trachemys scripta) were able to effectively reverse a direction habit, Holmes and Bitterman's 1966 study, using painted turtles (Chrysemys picta picta), discovered that even though the turtles were capable of preforming a spatial habit reversal they were unsuccessful at reversing a visual habit. Although the current study was not a traditional reversal paradigm it did require that the tortoises unlearn the association of the cue and reward from the previous LS to relearn the new cue and reward association in the next LSs. Like Holmes and Bitterman's animals, the tortoises in this study also seemed to be unable to reverse a visual habit (since the subjects did not show any evidence of a cue/reward association for the odor cue in any of the three LSs, whether the subjects would be capable of habit reversal involving an odor cue cannot be speculated on). Once the subjects had run the maze using the LS 1 cue, they appeared to have difficulty making new associations between the reward and the novel cues introduced in the next two LSs.

Even when only the data from LS 1, which would not have been confounded by possible interference, was analyzed, the first hypothesis, that the subjects would be able to employ all three cues to determine the location of the reward, was not supported. While both the light and landmark cue subjects showed an increase in their CGC from Increment 1 to Increment 12, only the light cue subjects showed statistical evidence that they came to associate the cue with the location of the reward. The subjects in the odor cue group, though, never seemed to make a connection between the cue and goal.

The second prediction, that the subjects would preform better using the landmark cue, was also not supported. While a divergence in cue use was apparent, it was the light cue group that exhibited, not only the most sizable increase in CGC between the first and last increments, but also the greatest percentage of CGC in Increment 12. Ultimately, the light cue subjects showed a stronger association between the cue and the reward and were able to determine the correct goalbox at a greater frequency than the other two groups.

There are several possible reasons why the findings of Experiment 1 did not agree with the hypothesis and why the light cue, not the landmark cue, was being used at a greater rate. Biegler and Morris (1996) explored the importance of landmark stability to spatial performance. In spatial arrangements that contained either fixed or shifting landmarks, these researchers established that rats' control over search location was lost when the landmark used to predict a reward was moved around within the trial arena. Biegler and Morris suggested that the animals were using spatial relationships among the reward and contextual cues, as well as the landmark cue, to determine a search location. When the landmark designating the reward was moved, it disrupted the correlation of the other cues to the reward and led to a reduction in learning.

Cheng's (1989) vector sum model also defines navigation as being based on relationships among several cues surrounding a goal. When a cue is repositioned, the animal's search pattern adjusts according to the weight placed on that cue. Cheng found that pigeons tended to place more weight on nearer landmarks vs. farther cues and would use the more heavily weighted cues to direct their search for the goal. Although external cues were controlled for in the current study, contextual cues of the maze itself could not be entirely eliminated. The maze sides and goalbox walls could have served as spatial cues for the tortoises while traversing the maze. Not only would the movement of the landmark cue from goalbox to goalbox have created the same disruption of spatial associations that Biegler and Morris investigated, but the maze walls would have been the nearest landmarks for the subjects to orient to. According to Cheng's vector sum model, the maze walls should have exerted more control over the tortoises' search patterns than the landmark cue and consequently guiding the subjects to the goalbox located at the end of the maze wall.

The suggestion that the movement of the landmark cue could cause disorientation in the tortoises is a valid one. In a tortoise's natural environment a landmark would represent a fixed feature, especially in a terrain as static as a desert, with the animal moving to approach it from various directions (Gallistel & Cramer, 1996). Although the animal may be viewing the landmark from a different angle, the relationship of the landmark to other features would remain constant. In the design of the current study, however, the moving landmark would be in conflict with natural occurrences and so provide a potential reason as to why the increase in CGC for the landmark cue was not significant. While some learning would occur, it would be impeded by the movement of the cue (Biegler & Morris, 1996).

Etienne, Maurer, and Séguinot (1996) also concluded that stable landmarks have an important impact on spatial abilities. In their study of mammal path integration and landmark interaction, they found that animals rely on an incorporation of path integration and stable landmarks to determine routes and locations of particular goals. In normal conditions, the use of landmarks is preferred over path integration to move within a familiar environment. However, when discrepancies in spatial representations occur, such as when a landmark is moved in relation to other cues, and learned external spatial references are no longer reliable, path integration becomes the dominant vector. As previously discussed, the movement of the landmark cue in the current study could have prevented the tortoises from establishing a conclusive association between the cue and the location of the reward. This may have resulted in the subjects trying to apply idiothetic coding to help pilot them to the goal. As dead reckoning is most effective when used in conjunction with reliable visual landmarks (Etienne et al., 1996; Gallistel & Cramer, 1996; Schöne, 1984), utilization of path integration would simply pilot the animals back to the previously visited goal box.

Although no research has been done on the desert tortoise's ability to use path integration, it is a plausible orientation strategy for this species. Several studies (Benhamou, Sauvé, & Bovet 1990; Bovet & Benhamou, 1988; Etienne et al., 1996) have suggested that the ability to utilize a path integration system for foraging would be an important adaptation for survival, especially for species that must forage from a central location (Etienne et al., 1996). The desert tortoise lives in a habitat that yields variable amounts of forage that is sporadically placed. In the high temperatures of the summer months the tortoise must locate the available food and then return quickly to shelter. Employing a navigational strategy that combines the use of landmarks and path integration would be the optimal method of foraging for this species. Unfortunately, the moving cue in the current study would obstruct such an approach to navigation as it would not be a reliable reference.

The movement of the light cue, however, may not have caused the same level of discrepancy among cues and reward as the movement of the landmark cue. Distal cues differ from proximal cues in that they do not directly indicate the location of the goal (Rudy, Stadler-Morris, & Albert, 1987; Schöne, 1984). Instead, distal cues rely on the spatial relationship of the cue relative to the goal in providing directional information to an animal. Although the landmark cue in the current study was located in front of the reward, it was not contiguous with the reward. Like a distal cue, in order for the subjects to effectively use the landmark cue they would need to establish a relationship between the landmark to other cues (i.e. the maze and goalbox walls) to determine the location of the reward. However, since the light cue was placed directly over the reward, it was contiguous with the goal, thus yielding more precise information for obtaining the reward.

It is, of course, also feasible that the light cue was simply a more salient cue for the tortoises. The brightness of the light may have created a greater contrast against the grey walls of the apparatus than the matte white of the wood block, so increasing its visibility. Had a colored block been used, the performance of the landmark subjects may have been enhanced as desert tortoises appear to have an acute sense of color (Grover & DeFalco, 1995; Okamoto, 1995; Woodbury & Hardy, 1948). The relative position of the two cues to the goalbox may have also been an important factor. Gopher tortoises have been found to have hyperopic tendencies (DeRosa & Taylor, 1980) and desert tortoises have been noted to react to a human approximately 60 m away (Grover & DeFalco, 1995). In the current study the subjects were often observed craning their necks upward while moving in the maze. This evidence of hyperopia would suggest that desert tortoises can effectively use distal cues, such as mountain ranges and the sun, for navigation and may have an innate predisposition to orient toward a higher cue. If so, it is likely that tortoises would naturally navigate towards cues that are above eye level and farther away, such as the light cue used in the current study. Another possibility is that the vertical shape of the landmark cue was difficult for the animals to distinguish against the goalbox walls and the use of a different shaped landmark may have been more effective.

Although it was conjectured that the subjects would be able to employ the odor cue to locate the reward, the subjects actually decreased their CGC across increments using the odor cue. Nevertheless, these result do not definitively indicate that the desert tortoise does not use odor cues within its environment. The current study required that the subjects use the spatial cues to locate a food reward, hence the findings can only be generalized to the animals' foraging behavior. Physiologically, chelonia appear to have a well developed olfactory system (Burghardt, 1970), and the desert tortoise is often seen "sniffing" the ground (Berry, 1986; Grover & DeFalco, 1995; Jennings, 1993). However, an odor is a chemical molecule attached to a fluid and then conveyed by advection and diffusion (Zimmer-Faust, Finelli, Pentcheff, & Wethey, 1995). Most chemosensory navigation is actually gradient navigation where the animal follows a trail of increasingly stronger odor cues until the goal is reached (Schöne, 1985). The limited amount of moisture available in the arid regions inhabited by the desert tortoise would severely limit the range of such a gradient, especially if the odors were emanating from plants evolved to restrict water loss. It would not be unreasonable to conclude then that attempting to locate desert vegetation through olfaction would not be profitable for the desert tortoise and the use of visual cues would be preferred for foraging. It is probable, however, that odor cues are important for locating mates, identifying home ranges and burrows, and determining that forage is safe.

The lack of significant results for the age comparison of CGC in Experiment 1 is not surprising for several reasons. An unequal distribution of the different ages in the three cue groups was produced for all three LSs. An analysis of the data in LS 1 could not be executed since the loss of subjects from the study left the landmark cue group without animals from the 3-year-old group. Consequently, the comparison was conducted using the data from all the LSs. As discussed earlier, the LS in which a cue was assigned to a subject affected the percentage of CGC for that subject. Therefore it can be presumed that, since none of the 3-year-olds were trained with the landmark cue in LS 1, the total landmark CGC would be low comparable to the other age groups and so confounding the results from the overall analysis.

Analysis of the subject’s goalbox position preferences yielded some intriguing findings. In the first LS the animals did show a preference for entering the right and left goalbox over the middle goalbox. These findings suggest that the subjects were using contextual cues while traversing the maze to compensate for the movement of the experimental cue. The maze walls would supply the subjects a stable landmark, similar to a trail, leading directly to either the right or left goalbox. If the maze walls were used in conjunction with the experimental cues, the combination could possibly provide an even more reliable predictor of the reward location than either spatial cue alone despite the movement of the experimental cue. Biegler and Morris (1996) determined that rats were still able to use paired landmarks as a predictor of a reward even when the pair was moved. If so, such use of the maze walls would suggest that following a trail is a potentially important spatial reference mechanism used in tortoise navigation and other cues are used to aid in determining which trail leads to the goal.

While the subjects entered the right and left goalboxes more often than the middle goalbox in LS 1, no such preferences were seen in LSs 2 and 3 as the subjects randomly chose among the three goalboxes. The lack of goalbox position preferences in LS 2 and 3 support the conjecture that the associations between cues and reward formed in LS 1 were causing interference for subsequent associations.

# EXPERIMENT 2

## Methods

### Procedures

The experiment started three days after the end of the last learning set in Experiment 1. The same subjects used in Experiment 1 were run using the same apparatus and spatial cues for 12 days of six trials per day. Each day consisted of three test trials and three retraining trials. Each test trial was followed by a retraining trial to prevent extinction of the maze running behavior. The order that each animal was run was randomly selected. For all trials, the animal was placed in the startbox with the door and lid in place. After 30 s the experimenter removed the door and lid and the animal was allowed to freely choose one of the three goalboxes. Each of the three goalboxes was marked by one of the three reference cues but no food was available. The order that the cues were assigned to the three goalboxes for each trial was counterbalanced. A cue choice (CC) was considered a subject entering and crossing the line at the end of the goalbox. The animal was then replaced into the startbox and the retraining trial was begun. An animal refusing to leave the start box after 3 min was returned to the startbox and the trial was considered a no-trial. The retraining trials were run the same as the trials in

Experiment 1 except all three cues were used for each subject on all trial days so that each subject was retrained an equal number of times for each cue. The goalbox order for each retraining trial was counterbalanced. Experiment 2 was completed when all subjects had participated in all test and retraining trials.

## Results

The data from Experiment 2 was prepared for analysis by dividing the 12 days into four blocks of three days and calculating the percentage of times that each cue was chosen during the test trials for each group. The transformed data was then tested using a one-way ANOVA. Only a marginally significant difference in CC was found among the landmark, light and odor cue means, $F(2, 22) = 3.36$, $p = .053$. An examination of the within-subjects contrasts, nevertheless, found that the deviation between the landmark and the odor cue CCs was significant, $F(1, 11) = 9.06$, $p = .01$. A bar graph depicting the CC means (see Figure 5) illustrates, that while the light and odor cue were chosen at an almost equal rate, the choice of the landmark cue fell significantly below chance selection.

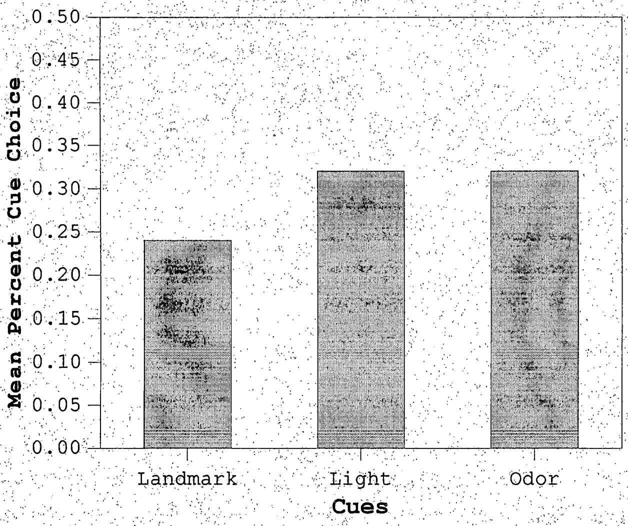

Figure 5. Mean percent of cue choice for all test trials.

When a 3 x 3 (age x cue) mixed ANOVA with repeated measures was run to investigate for possible age differences, a significant variation in CCs was found among the means of the cue main effect (see Table 5), and the within-subject contrasts show that the light and landmark cue means, as well as the landmark and odor cue means differed significantly, Fs(1, 9) = 5.09 and 9.09, $p < .05$, in order. There was no significance for the age main effect or for an interaction, though Figure 6 does show that the light and landmark cue fluctuated slightly by age.

Table 5

Analysis of Variance for Cue Choice by Subject Age

| | | _F_ |
|---|---|---|
| Source | _df_ | CC |
| | Between subjects | |
| Age (A) | 2 | 0.50 |
| Error | 9 | (.0006) |
| | Within subjects | |
| Cue(C) | 2 | 4.38* |
| C x A | 4 | 2.69 |
| Error | 18 | (.005) |

_Note_. Values in parenthesis represent mean square errors. CC = cue choice.

*_p_ < .05. **_p_ < .01.

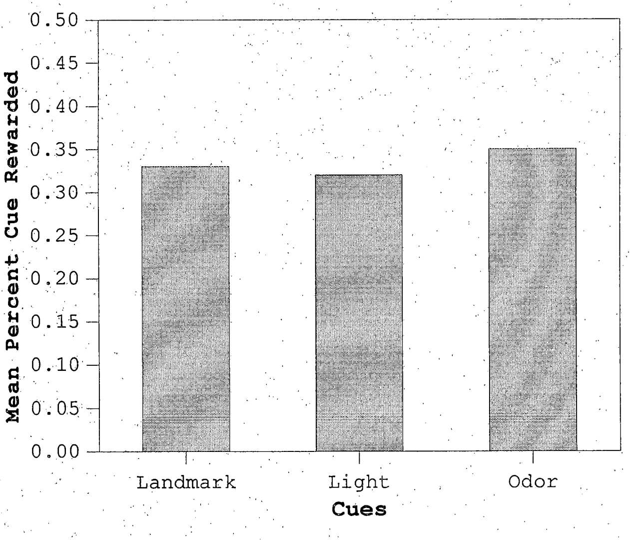

Figure 6. Mean percent of cue choice by age for all test trials.

The percent of times each subject was rewarded for each cue in the retraining trials was also examined, as this could be a possible indication of cue learning. A one-way ANOVA used to test the data found that there was no significant main effect for cue reward, nor were there any significant differences found between the means when the within-subject contrasts were inspected. A bar graph of the cue reward means (see Figure 7) shows that the percent the subjects were rewarded for the corrrect response was only at approximately chance level.

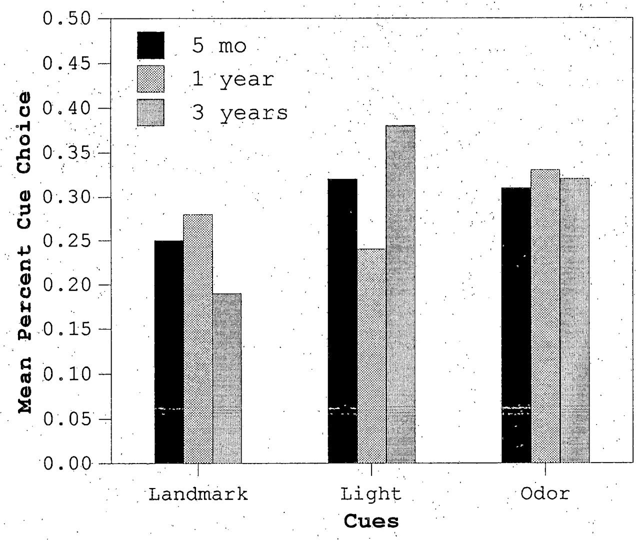

Figure 7. Mean percent of rewarded cue choice in all retraining trials.

Table 6 shows the results from a 3 x 3 (age x cue) mixed ANOVA with repeated measures that was applied to test for age differences in cue reward. No significance was found for the cue or age main effects, or for the interaction. A bar graph of the means (see Figure 8), however, shows that, though the subjects were rewarded for using the landmark cue at a consistent amount for all three age groups, the percentage that the subjects were rewarded for using the light and the odor cue fluctuated slightly by age.

Table 6

Analysis of Variance for Rewarded Cue Choice by Subject Age

| Source | df | F |
|---|---|---|
| | | CR |
| Between subjects | | |
| Age (A) | 2 | 0.14 |
| Error | 9 | (.005) |
| Within subjects | | |
| Cue(C) | 2 | 0.92 |
| C x A | 4 | 0.24 |
| Error | 18 | (.002) |

Note. Values in parenthesis represent mean square errors. CR = cue reward.

*$p < .05$. **$p < .01$.

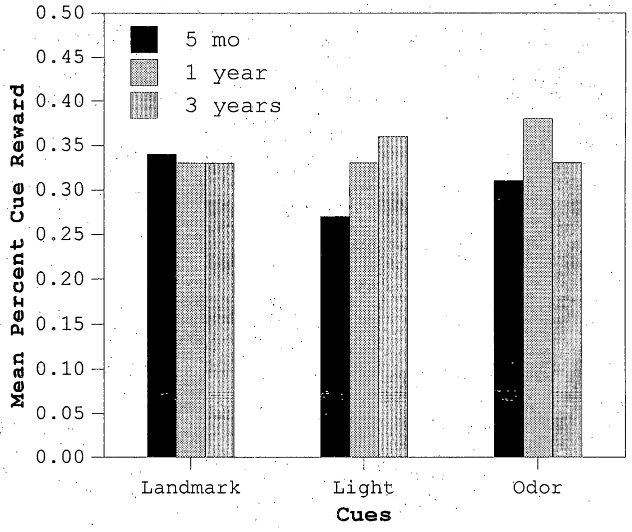

Figure 8. Mean percent of rewarded cue choice by age for all retraining trials.

## Discussion

Although it was expected that the subjects would demonstrate a preference for the landmark cue when all three cues were presented together, this hypothesis was not supported by the data from Experiment 2. Conversely, the landmark cue was chosen the least, and surprisingly, in contrast to the findings in Experiment 1, the subjects selected the odor cue the highest percentage of times. It is believed, however, that the design of the current study led to these contradictory findings. The overall higher percentage of odor CC may not be due to a preference for the odor cue but to an extinction of the associations between the spatial cues and the rewards. Overtraining has been theorized as increasing the rate of extinction, though the elements contributing to this phenomenon are unclear (Mackintosh, 1974, p. 423-431). If such a theory has validity, than the considerable number of trials the subjects underwent in Experiment 1 should have influenced the results of Experiment 2 and accelerated the extinction rate of the cue/reward association. The magnitude of the reward in Experiment 1 might have also affected the extinction rate. Mackintosh cited a study by Pert and Bitterman (1970) that found that large rewards inhibited extinction in turtles. In the current study, however, only a small reward was available to the subjects, so such an inhibition would not have occurred. It can also be speculated that the interference experienced in LSs 2 and 3 had a notable effect on the data of Experiment 2, affecting both the extinction rate of any association and the subjects' ability to grasp what was being required of them in Experiment 2.

The cue that was chosen by the subjects in the first trial of Experiment 2, however, did yield some interesting findings. As the subjects had recently concluded the training trials of Experiment 1, it would be expected that if the subjects had developed any association between the spatial cue and reward in the last LS then the subjects would enter the goalbox marked by that cue. This was true for the landmark cue group and all but one subject in the light cue group (a total of five subjects), but only one subject from the odor cue group chose to enter the goalbox designated by the odor cue on the first trial. The remaining five subjects selected the goalbox that was marked by the assigned cue from LS 1. While it is not possible to formulate a solid conclusion from such limited data, these findings agree with the findings in Experiment 1 that the light and landmark cues were more salient to the subjects then the odor cue and strengthens the assertion that odor may not be used as a spatial cue by the tortoise while foraging.

Although there was no significant difference in CC among the cues, the slight age differences depicted in the graph suggests that age variations in cue use may exist. Such a possibility needs to be further examined.

It was hoped that an analysis of the percent a subject was rewarded for using a cue in the retraining trials would also provide an indication as to which cues were being employed by the subjects to locate the reward. The premise used was if the animals had made a sufficient association between a cue and the reward then the subjects would continue to utilize that cue to obtain the reward in the retraining trials. Unfortunately, there was no evidence of such an association as the subjects were rewarded for using each cue at chance level.

# GENERAL DISCUSSION AND IMPLICATIONS

Desert tortoises appear to have a reliable understanding of their home ranges and are able to locate essential features in their habitats efficiently (Berry, 1986; Grover & DeFalco, 1995; Jennings, 1993). The findings of the first experiment study suggest that this species uses a light cue for foraging. The light, however, could have represented several types of visual spatial cues to the animals, such a distal landmark (i.e., mountain ranges), as it was placed above eye level, or the polarized light of the sun at the horizon (Schöne, 1984; Waterman, 1989). Although the light in the current experiment did not replicate the sun's movement, the use of the light could have also indicated the subjects' ability to navigate using a sun compass, as the horizontal motion of a light bulb has been found to elicited orientation behavior similar to that caused by the sun in honey bees (Waterman, 1989).

To understand the desert tortoise's navigational proficiencies fully, determining how the light cue was being employed is necessary. If the desert tortoise is found to only use a light analogous to a landmark it would suggest that they employ piloting, or use familiar landmarks, to establish their position. However, using the light as a celestial cue would indicate that this species is capable of compensating for the movement of the sun and can use true navigation, which is the ability to use the relationship between two independent reference points to establish a correct route (DeRosa & Taylor, 1980; Schöne, 1984; Waterman, 1989). To determine whether a species uses sun compass navigation, a clock-shift experiment can be administered (Waterman, 1989). A clock-shift experiment involves training the subject to locate a goal at a particular time of day so that the goal is located at a specific angle to the sun. The animal's internal clock is than manipulated by delaying the subject's exposure to the day-night schedule. When the animal is returned to the experimental arena, the direction the subject takes to locate the goal is noted. If the animal is capable of using a sun compass, then the goal should be miscalculated by the degree of sun rotation corresponding to the time delay. If, however, the subject returns to the original goal position, this would suggest that the animal is using some other cue for orientation.

The desert tortoise might also use distal cues, such as the light cue in this study, in conjunction with trails and proximal landmarks to provide more precise information as to the location of the goal. Such a possibility was indicated by the data of Experiment 1 and needs to be investigated.

There is the potential that the light cue was only being used by the subjects to strengthen the spatial information provided by the context cues of the maze and is not a primary spatial cue for the tortoise.

More conclusive tests also need to be run on the desert tortoise's use of landmarks. Studies using landmark conditions, such as a static landmark or landmarks in pairs, that have been shown to allow subjects to form robust spatial associations need to be applied as the moving landmark condition in the current study has been evidenced as impeding learning (Biegler & Morris, 1996). Other landmark features, such as magnitude, shape, and color need to be explored as well. It is possible that the desert tortoise relies more on certain categories of landmarks (i.e., large rocks vs. bushes), as they represent more stable components of the environment.

Lastly, studies need to be done using additional rewards besides food, as the spatial cues used in foraging may be dissimilar from the cues used to locate other needed resources. It is feasible that odor plays an important part in locating water and mates. Since water is such a transient commodity in a desert, the use of landmarks or sun compass orientation may not be the most practical method for determining its locality. While both of these spatial cues would orient the tortoises to where water is often found, neither landmarks or sun compass orientation would provide information as to its availability. Following an odor gradient, however, would not only lead the animals to the location of water, but would also help ensure that water would be accessible. This would be an important adaptation in an environment where stored body resources depleted by travel would be difficult to replace. The search for mates might also be facilitated by the use of odors. Tortoises have been shown to use several burrows within their home ranges (Jennings, 1993). By using odors emitted from the female's cloaca, the male would be provided with a trial that lead to her exact location without needlessly expending energy.

Although the findings of this study were inconclusive as to the desert tortoise's use of light, landmark, and odor cues, it was indicated that there is a difference in spatial cue use by this species. Such variations in cue use need to be investigated, as these diverse methods of course keeping could have very different consequences on relocation attempts. Persons involved in such projects need to consider what cues are being used by the tortoises to move productively through their habitat. Not taking into account such cues or allowing time for the animals to orient to them could cause the loss of tortoises from the new sites. If tortoises are orienting to proximal landmarks then the animals could be moving off relocation sites in search of familiar landmarks. Additionally, if tortoises are capable of true navigation, then relocation projects face an even greater challenge in preventing the animals from returning to areas that are no longer appropriate habitat as moving the animals to areas that are too close to their original home territories may enable the tortoise to use distal cues or sun compass orientation to move back to their initial sites.

This study also presented unexpected information concerning the desert tortoise's spatial learning abilities that could effect relocation projects. The indication that the subjects had difficulty in relearning the maze using a new spatial cue could signify that the tortoises would have a difficult time relearning a new natural habitat. Animals that must be held in enclosures before being released into relocation sites could be at an even greater disadvantage and take longer to adapt to their destination then animals moved directly to their new home areas. The age of the animal could also be a factor in their ability to adjust to a new location. Hatchlings that have never established a spatial representation of an area may relocate with less difficultly than older animals that have acquired substantial knowledge of their first environment.

It is essential that all of these factors are investigated if relocation efforts are to be effective. Until such time, however, the fact that the desert tortoise does have a spatial awareness of their environment needs to be considered. It is reasonable to assume that relocated animals will experience disorientation and attempt to find familiar spatial cues that will inform them of their location. As a solution, confining the animals in their new areas would prevent the animals from moving off-site and allow them to familiarize themselves with the features of their new habitat. Such strategies may enable relocated tortoises to become established in habitats that will enable them to reproduce successfully and thrive, thus allowing them to be removed as a threatened species from the Federal Endangered Species Act (Federal Register, 1994).

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| | cue | age | set# | trial1 | trial2 | trial3 | trial4 |
|---|---|---|---|---|---|---|---|
| 1 | light | 1 yr | 1st | .36 | .33 | .37 | .43 |
| 2 | light | 5 mo | 1st | .25 | .27 | .60 | .40 |
| 3 | light | 3 yr | 1st | .43 | .25 | .25 | .44 |
| 4 | light | 3 yr | 1st | .22 | .30 | .10 | .30 |
| 5 | landmark | 1 yr | 1st | .25 | .24 | .21 | .33 |
| 6 | landmark | 1 yr | 1st | .42 | .33 | .33 | .30 |
| 7 | landmark | 5 mo | 1st | .23 | .22 | .37 | .28 |
| 8 | landmark | 5 mo | 1st | .33 | .29 | .34 | .33 |
| 9 | landmark | 1 yr | 1st | .00 | .00 | .34 | .21 |

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|  | trial5 | trial6 | trial7 | trial8 | trial9 | trial10 | trial11 | trial12 |
|---|---|---|---|---|---|---|---|---|
| 1 | .33 | .37 | .41 | .41 | .40 | .46 | .53 | .63 |
| 2 | .42 | .45 | .41 | .17 | .39 | .47 | .40 | .79 |
| 3 | .27 | .32 | .30 | .56 | .35 | .43 | .43 | .58 |
| 4 | .33 | .41 | .44 | .29 | .17 | .41 | .48 | .42 |
| 5 | .23 | .47 | .40 | .42 | .30 | .47 | .53 | .63 |
| 6 | .20 | .47 | .42 | .42 | .48 | .47 | .50 | .53 |
| 7 | .52 | .37 | .17 | .41 | .33 | .40 | .33 | .36 |
| 8 | .33 | .37 | .40 | .46 | .48 | .42 | .47 | .48 |
| 9 | .33 | .27 | .35 | .30 | .43 | .53 | .63 | .71 |

|  | cue | age | set# | trial1 | trial2 | trial3 | trial4 |
|---|---|---|---|---|---|---|---|
| 10 | odor | 1 yr | 3rd | .25 | .43 | .40 | .36 |
| 11 | odor | 3 yr | 3rd | .58 | .40 | .43 | .40 |
| 12 | odor | 1 yr | 3rd | .46 | .33 | .57 | .47 |
| 13 | odor | 1 yr | 3rd | .32 | .33 | .43 | .57 |
| 14 | odor | 5 mo | 3rd | .30 | .20 | .67 | .40 |
| 15 | odor | 5 mo | 3rd | .42 | .40 | .57 | .43 |
| 16 | light | 1 yr | 3rd | .42 | .33 | .63 | .46 |
| 17 | light | 5 mo | 3rd | .31 | .27 | .71 | .40 |
| 18 | light | 5 mo | 3rd | .50 | .37 | .57 | .43 |

|  | trial5 | trial6 | trial7 | trial8 | trial9 | trial10 | trial11 | trial12 |
|---|---|---|---|---|---|---|---|---|
| 10 | .33 | .50 | .52 | .40 | .33 | .30 | .33 | .33 |
| 11 | .25 | .33 | .37 | .29 | .40 | .31 | .33 | .50 |
| 12 | .27 | .33 | .30 | .33 | .43 | .37 | .47 | .30 |
| 13 | .29 | .31 | .29 | .31 | .31 | .33 | .28 | .31 |
| 14 | .33 | .29 | .35 | .33 | .37 | .37 | .35 | .29 |
| 15 | .27 | .37 | .27 | .32 | .27 | .17 | .40 | .29 |
| 16 | .46 | .46 | .46 | .46 | .46 | .46 | .46 | .46 |
| 17 | .43 | .25 | .36 | .27 | .32 | .33 | .50 | .42 |
| 18 | .31 | .31 | .32 | .43 | .47 | .43 | .57 | .54 |

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|  | cue | age | set# | trial1 | trial2 | trial3 | trial4 |
|---|---|---|---|---|---|---|---|
| 19 | light | 3 yr | 3rd | .43 | .35 | .53 | .47 |
| 20 | landmark | 1 yr | 3rd | .07 | .30 | .17 | .23 |
| 21 | landmark | 3 yr | 3rd | .42 | .27 | .50 | .46 |
| 22 | light | 1 yr | 2nd | .33 | .33 | .27 | .23 |
| 23 | light | 1 yr | 2nd | .50 | .40 | .28 | .50 |
| 24 | light | 5 mo | 2nd | .37 | .40 | .45 | .43 |
| 25 | light | 1 yr | 2nd | .37 | .27 | .18 | .28 |
| 26 | landmark | 3 yr | 2nd | .33 | .23 | .27 | .20 |
| 27 | landmark | 1 yr | 2nd | .43 | .43 | .30 | .21 |

| | trial5 | trial6 | trial7 | trial8 | trial9 | trial10 | trial11 | trial12 |
|---|---|---|---|---|---|---|---|---|
| 19 | .31 | .29 | .28 | .14 | .40 | .36 | .35 | .33 |
| 20 | .50 | .23 | .20 | .17 | .19 | .13 | .25 | .17 |
| 21 | .40 | .33 | .30 | .33 | .37 | .37 | .28 | .29 |
| 22 | .37 | .25 | .40 | .33 | .37 | .37 | .30 | .37 |
| 23 | .43 | .38 | .30 | .33 | .37 | .25 | .83 | .39 |
| 24 | .19 | .47 | .33 | .33 | .53 | .43 | .47 | .50 |
| 25 | .28 | .31 | .19 | .27 | .32 | .13 | .26 | .00 |
| 26 | .22 | .32 | .27 | .25 | .33 | .27 | .40 | .25 |
| 27 | .23 | .33 | .38 | .47 | .40 | .37 | .39 | .37 |

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|  | cue | age | set# | trial1 | trial2 | trial3 | trial4 |
|---|---|---|---|---|---|---|---|
| 28 | landmark | 5 mo | 2nd | .23 | .30 | .23 | .21 |
| 29 | landmark | 3 yr | 2nd | .38 | .39 | .19 | .28 |
| 30 | landmark | 5 mo | 2nd | .37 | .57 | .43 | .27 |
| 31 | odor | 1 yr | 1st | .40 | .00 | .20 | .33 |
| 32 | odor | 5 mo | 1st | .38 | .30 | .37 | .37 |
| 33 | odor | 3 yr | 1st | .39 | .41 | .32 | .40 |
| 34 | odor | 1 yr | 2nd | .23 | .38 | .50 | .17 |
| 35 | odor | 5 mo | 2nd | .38 | .50 | .26 | .25 |
| 36 | odor | 3 yr | 2nd | .26 | .37 | .40 | .40 |

|  | trial5 | trial6 | trial7 | trial8 | trial9 | trial10 | trial11 | trial12 |
|---|---|---|---|---|---|---|---|---|
| 28 | .43 | .37 | .21 | .33 | .33 | .40 | .33 | .33 |
| 29 | .13 | .35 | .20 | .25 | .46 | .37 | .30 | .41 |
| 30 | .33 | .27 | .47 | .41 | .30 | .20 | .50 | .43 |
| 31 | .39 | .21 | .33 | .45 | .14 | .30 | .39 | .30 |
| 32 | .38 | .47 | .40 | .29 | .46 | .46 | .37 | .33 |
| 33 | .18 | .27 | .50 | .43 | .37 | .37 | .35 | .30 |
| 34 | .30 | .24 | .37 | .40 | .27 | .23 | .39 | .37 |
| 35 | .33 | .15 | .32 | .31 | .26 | .13 | .24 | .50 |
| 36 | .56 | .33 | .23 | .18 | .43 | .47 | .38 | .33 |

## Cue x Increments

**Descriptive Statistics**

| | cue | Mean | Std. Deviation | N |
|---|---|---|---|---|
| TRIAL1 | landmark | .2883 | .1389 | 12 |
| | light | .3742 | 8.82E-02 | 12 |
| | odor | .3642 | 9.97E-02 | 12 |
| | Total | .3422 | .1146 | 36 |
| TRIAL2 | landmark | .2975 | .1364 | 12 |
| | light | .3225 | 5.15E-02 | 12 |
| | odor | .3375 | .1298 | 12 |
| | Total | .3192 | .1107 | 36 |
| TRIAL3 | landmark | .3067 | 9.92E-02 | 12 |
| | light | .4117 | .1974 | 12 |
| | odor | .4267 | .1351 | 12 |
| | Total | .3817 | .1550 | 36 |
| TRIAL4 | landmark | .2758 | 7.46E-02 | 12 |
| | light | .3975 | 8.31E-02 | 12 |
| | odor | .3792 | .1010 | 12 |
| | Total | .3508 | .1004 | 36 |
| TRIAL5 | landmark | .3208 | .1235 | 12 |
| | light | .3442 | 8.02E-02 | 12 |
| | odor | .3233 | 9.39E-02 | 12 |
| | Total | .3294 | 9.85E-02 | 36 |
| TRIAL6 | landmark | .3458 | 7.30E-02 | 12 |
| | light | .3558 | 7.90E-02 | 12 |
| | odor | .3167 | 9.93E-02 | 12 |
| | Total | .3394 | 8.38E-02 | 36 |
| TRIAL7 | landmark | .3142 | .1026 | 12 |
| | light | .3500 | 7.79E-02 | 12 |
| | odor | .3542 | 8.67E-02 | 12 |
| | Total | .3394 | 8.89E-02 | 36 |
| TRIAL8 | landmark | .3517 | 9.49E-02 | 12 |
| | light | .3325 | .1193 | 12 |
| | odor | .3367 | 7.40E-02 | 12 |
| | Total | .3403 | 9.54E-02 | 36 |
| TRIAL9 | landmark | .3667 | 8.72E-02 | 12 |
| | light | .3792 | 9.06E-02 | 12 |
| | odor | .3367 | 9.20E-02 | 12 |
| | Total | .3608 | 8.92E-02 | 36 |
| TRIAL10 | landmark | .3667 | .1153 | 12 |
| | light | .3775 | .1007 | 12 |
| | odor | .3175 | .1032 | 12 |
| | Total | .3539 | .1069 | 36 |
| TRIAL11 | landmark | .4092 | .1170 | 12 |
| | light | .4650 | .1471 | 12 |
| | odor | .3567 | 5.93E-02 | 12 |
| | Total | .4103 | .1192 | 36 |
| TRIAL12 | landmark | .4133 | .1555 | 12 |
| | light | .4525 | .1917 | 12 |
| | odor | .3458 | 7.55E-02 | 12 |
| TRIAL12 | Total | .4039 | .1515 | 36 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1

Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| FACTOR1 | .324 | 11 | 2.9E-02 | 2.844 | .001 | 31.282 | .982 |
| FACTOR1 * CUE | .336 | 22 | 1.5E-02 | 1.475 | .079 | 32.448 | .944 |
| Error(FACTOR1) | 3.760 | 363 | 1.0E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| FACTOR1 | FACTOR1_1 | 1.9E-02 | 1 | 1.9E-02 | 1.261 | .270 | 1.261 | .193 |
| | FACTOR1_2 | 5.6E-02 | 1 | 5.6E-02 | 1.817 | .187 | 1.817 | .258 |
| | FACTOR1_3 | 2.7E-03 | 1 | 2.7E-03 | .218 | .643 | .218 | .074 |
| | FACTOR1_4 | 5.9E-03 | 1 | 5.9E-03 | .187 | .668 | .187 | .070 |
| | FACTOR1_5 | 2.8E-04 | 1 | 2.8E-04 | .015 | .902 | .015 | .052 |
| | FACTOR1_6 | 2.8E-04 | 1 | 2.8E-04 | .014 | .907 | .014 | .052 |
| | FACTOR1_7 | 1.4E-04 | 1 | 1.4E-04 | .009 | .925 | .009 | .051 |
| | FACTOR1_8 | 1.2E-02 | 1 | 1.2E-02 | .922 | .344 | .922 | .154 |
| | FACTOR1_9 | 4.9E-03 | 1 | 4.9E-03 | .191 | .665 | .191 | .071 |
| | FACTOR1_10 | .167 | 1 | .167 | 7.211 | .011 | 7.211 | .741 |
| | FACTOR1_11 | .137 | 1 | .137 | 3.700 | .063 | 3.700 | .463 |
| FACTOR1 * CUE | FACTOR1_1 | 2.2E-02 | 2 | 1.1E-02 | .739 | .485 | 1.479 | .165 |
| | FACTOR1_2 | 1.2E-02 | 2 | 5.9E-03 | .191 | .827 | .382 | .077 |
| | FACTOR1_3 | 8.4E-03 | 2 | 4.2E-03 | .345 | .711 | .690 | .101 |
| | FACTOR1_4 | 3.8E-02 | 2 | 1.9E-02 | .598 | .556 | 1.195 | .141 |
| | FACTOR1_5 | 7.1E-02 | 2 | 3.5E-02 | 1.961 | .157 | 3.922 | .377 |
| | FACTOR1_6 | 1.6E-02 | 2 | 8.0E-03 | .399 | .674 | .798 | .109 |
| | FACTOR1_7 | 7.8E-02 | 2 | 3.9E-02 | 2.597 | .090 | 5.193 | .481 |
| | FACTOR1_8 | 7.1E-02 | 2 | 3.5E-02 | 2.608 | .089 | 5.216 | .483 |
| | FACTOR1_9 | 9.5E-02 | 2 | 4.8E-02 | 1.853 | .173 | 3.705 | .358 |
| | FACTOR1_10 | .108 | 2 | 5.4E-02 | 2.339 | .112 | 4.678 | .440 |
| | FACTOR1_11 | .128 | 2 | 6.4E-02 | 1.733 | .192 | 3.467 | .337 |
| Error(FACTOR1) | FACTOR1_1 | .501 | 33 | 1.5E-02 | | | | |
| | FACTOR1_2 | 1.017 | 33 | 3.1E-02 | | | | |
| | FACTOR1_3 | .403 | 33 | 1.2E-02 | | | | |
| | FACTOR1_4 | 1.038 | 33 | 3.1E-02 | | | | |
| | FACTOR1_5 | .593 | 33 | 1.8E-02 | | | | |
| | FACTOR1_6 | .659 | 33 | 2.0E-02 | | | | |
| | FACTOR1_7 | .495 | 33 | 1.5E-02 | | | | |
| | FACTOR1_8 | .446 | 33 | 1.4E-02 | | | | |
| | FACTOR1_9 | .846 | 33 | 2.6E-02 | | | | |
| | FACTOR1_10 | .763 | 33 | 2.3E-02 | | | | |
| | FACTOR1_11 | 1.221 | 33 | 3.7E-02 | | | | |

a. Computed using alpha = .05

### Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 4.561 | 1 | 4.561 | 1790.181 | .000 | 1790.181 | 1.000 |
| CUE | 1.1E-02 | 2 | 5.7E-03 | 2.235 | .123 | 4.471 | .423 |
| Error | 8.4E-02 | 33 | 2.5E-03 | | | | |

a. Computed using alpha = .05

## Age x Increments

### Descriptive Statistics

|  | age | Mean | Std. Deviation | N |
|---|---|---|---|---|
| TRIAL1 | 5 mo | .3392 | 8.08E-02 | 12 |
|  | 1 yr | .3207 | .1408 | 15 |
|  | 3 yr | .3822 | .1056 | 9 |
|  | Total | .3422 | .1146 | 36 |
| TRIAL2 | 5 mo | .3408 | .1112 | 12 |
|  | 1 yr | .2953 | .1309 | 15 |
|  | 3 yr | .3300 | 6.87E-02 | 9 |
|  | Total | .3192 | .1107 | 36 |
| TRIAL3 | 5 mo | .4642 | .1580 | 12 |
|  | 1 yr | .3453 | .1404 | 15 |
|  | 3 yr | .3322 | .1442 | 9 |
| TRIAL3 | Total | .3817 | .1550 | 36 |
| TRIAL4 | 5 mo | .3500 | 7.89E-02 | 12 |
|  | 1 yr | .3387 | .1226 | 15 |
|  | 3 yr | .3722 | 9.19E-02 | 9 |
|  | Total | .3508 | .1004 | 36 |
| TRIAL5 | 5 mo | .3558 | 8.65E-02 | 12 |
|  | 1 yr | .3293 | 8.72E-02 | 15 |
|  | 3 yr | .2944 | .1282 | 9 |
|  | Total | .3294 | 9.85E-02 | 36 |
| TRIAL6 | 5 mo | .3450 | 9.62E-02 | 12 |
|  | 1 yr | .3420 | 9.65E-02 | 15 |
|  | 3 yr | .3278 | 3.90E-02 | 9 |
|  | Total | .3394 | 8.38E-02 | 36 |
| TRIAL7 | 5 mo | .3342 | 8.56E-02 | 12 |
|  | 1 yr | .3547 | 8.97E-02 | 15 |
|  | 3 yr | .3211 | 9.79E-02 | 9 |
|  | Total | .3394 | 8.89E-02 | 36 |
| TRIAL8 | 5 mo | .3383 | 7.99E-02 | 12 |
|  | 1 yr | .3647 | 8.27E-02 | 15 |
|  | 3 yr | .3022 | .1277 | 9 |
|  | Total | .3403 | 9.54E-02 | 36 |
| TRIAL9 | 5 mo | .3758 | 8.97E-02 | 12 |
|  | 1 yr | .3467 | 9.60E-02 | 15 |
|  | 3 yr | .3644 | 8.31E-02 | 9 |
|  | Total | .3608 | 8.92E-02 | 36 |
| TRIAL10 | 5 mo | .3508 | .1180 | 12 |
|  | 1 yr | .3447 | .1233 | 15 |
|  | 3 yr | .3733 | 6.00E-02 | 9 |
|  | Total | .3539 | .1069 | 36 |
| TRIAL11 | 5 mo | .4108 | 9.35E-02 | 12 |
|  | 1 yr | .4360 | .1564 | 15 |
|  | 3 yr | .3667 | 6.32E-02 | 9 |
|  | Total | .4103 | .1192 | 36 |
| TRIAL12 | 5 mo | .4383 | .1406 | 12 |
|  | 1 yr | .3913 | .1832 | 15 |
|  | 3 yr | .3789 | .1080 | 9 |
|  | Total | .4039 | .1515 | 36 |

### Tests of Within-Subjects Effects

Measure: MEASURE_1

Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| FACTOR1 | .290 | 11 | 2.6E-02 | 2.476 | .005 | 27.240 | .961 |
| FACTOR1 * AGE | .230 | 22 | 1.0E-02 | .982 | .487 | 21.604 | .772 |
| Error(FACTOR1) | 3.866 | 363 | 1.1E-02 |  |  |  |  |

a. Computed using alpha = .05

**Tests of Within-Subjects Contrasts**

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power^a |
|---|---|---|---|---|---|---|---|---|
| FACTOR1 | FACTOR1_1 | 2.2E-02 | 1 | 2.2E-02 | 1.433 | .240 | 1.433 | .213 |
| | FACTOR1_2 | 3.8E-02 | 1 | 3.8E-02 | 1.450 | .237 | 1.450 | .215 |
| | FACTOR1_3 | 1.4E-03 | 1 | 1.4E-03 | .110 | .742 | .110 | .062 |
| | FACTOR1_4 | 1.5E-02 | 1 | 1.5E-02 | .489 | .489 | .489 | .104 |
| | FACTOR1_5 | 2.8E-03 | 1 | 2.8E-03 | .149 | .702 | .149 | .066 |
| | FACTOR1_6 | 3.9E-03 | 1 | 3.9E-03 | .209 | .651 | .209 | .073 |
| | FACTOR1_7 | 5.2E-03 | 1 | 5.2E-03 | .352 | .557 | .352 | .089 |
| | FACTOR1_8 | 7.7E-03 | 1 | 7.7E-03 | .509 | .481 | .509 | .107 |
| | FACTOR1_9 | 2.7E-03 | 1 | 2.7E-03 | .097 | .758 | .097 | .061 |
| | FACTOR1_10 | .113 | 1 | .113 | 4.796 | .036 | 4.796 | .566 |
| | FACTOR1_11 | .106 | 1 | .106 | 2.709 | .109 | 2.709 | .359 |
| FACTOR1 * AGE | FACTOR1_1 | 1.5E-02 | 2 | 7.5E-03 | .489 | .617 | .979 | .123 |
| | FACTOR1_2 | .163 | 2 | 8.2E-02 | 3.108 | .058 | 6.217 | .559 |
| | FACTOR1_3 | 4.5E-03 | 2 | 2.2E-03 | .182 | .834 | .364 | .076 |
| | FACTOR1_4 | 6.8E-02 | 2 | 3.4E-02 | 1.112 | .341 | 2.224 | .229 |
| | FACTOR1_5 | 3.4E-02 | 2 | 1.7E-02 | .881 | .424 | 1.762 | .189 |
| | FACTOR1_6 | 5.1E-02 | 2 | 2.5E-02 | 1.348 | .274 | 2.697 | .270 |
| | FACTOR1_7 | 8.7E-02 | 2 | 4.3E-02 | 2.934 | .067 | 5.869 | .533 |
| | FACTOR1_8 | 1.7E-02 | 2 | 8.3E-03 | .549 | .583 | 1.098 | .133 |
| | FACTOR1_9 | 6.1E-03 | 2 | 3.0E-03 | .107 | .899 | .215 | .065 |
| | FACTOR1_10 | 9.7E-02 | 2 | 4.8E-02 | 2.058 | .144 | 4.116 | .393 |
| | FACTOR1_11 | 5.6E-02 | 2 | 2.8E-02 | .716 | .496 | 1.432 | .161 |
| Error(FACTOR1) | FACTOR1_1 | .508 | 33 | 1.5E-02 | | | | |
| | FACTOR1_2 | .866 | 33 | 2.6E-02 | | | | |
| | FACTOR1_3 | .407 | 33 | 1.2E-02 | | | | |
| | FACTOR1_4 | 1.008 | 33 | 3.1E-02 | | | | |
| | FACTOR1_5 | .630 | 33 | 1.9E-02 | | | | |
| | FACTOR1_6 | .624 | 33 | 1.9E-02 | | | | |
| | FACTOR1_7 | .486 | 33 | 1.5E-02 | | | | |
| | FACTOR1_8 | .500 | 33 | 1.5E-02 | | | | |
| | FACTOR1_9 | .935 | 33 | 2.8E-02 | | | | |
| | FACTOR1_10 | .775 | 33 | 2.3E-02 | | | | |
| | FACTOR1_11 | 1.293 | 33 | 3.9E-02 | | | | |

a. Computed using alpha = .05

**Tests of Between-Subjects Effects**

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power^a |
|---|---|---|---|---|---|---|---|
| Intercept | 4.356 | 1 | 4.356 | 1569.103 | .000 | 1569.103 | 1.000 |
| AGE | 3.9E-03 | 2 | 1.9E-03 | .694 | .507 | 1.388 | .157 |
| Error | 9.2E-02 | 33 | 2.8E-03 | | | | |

a. Computed using alpha = .05

## Landmark x Increment

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| TRIALS | .269 | 11 | 2.4E-02 | 2.279 | .014 | 25.069 | .929 |
| Error(TRIALS) | 1.300 | 121 | 1.1E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | .231 | 1 | .231 | 5.116 | .045 | 5.116 | .541 |
| | TRIALS_2 | 1.2E-02 | 1 | 1.2E-02 | 1.432 | .257 | 1.432 | .194 |
| | TRIALS_3 | 2.6E-05 | 1 | 2.6E-05 | .002 | .965 | .002 | .050 |
| | TRIALS_4 | 4.1E-06 | 1 | 4.1E-06 | .002 | .966 | .002 | .050 |
| | TRIALS_5 | 1.5E-05 | 1 | 1.5E-05 | .002 | .964 | .002 | .050 |
| | TRIALS_6 | 4.0E-03 | 1 | 4.0E-03 | .378 | .551 | .378 | .087 |
| | TRIALS_7 | 2.0E-04 | 1 | 2.0E-04 | .024 | .880 | .024 | .052 |
| | TRIALS_8 | 6.4E-05 | 1 | 6.4E-05 | .011 | .917 | .011 | .051 |
| | TRIALS_9 | 1.8E-02 | 1 | 1.8E-02 | 7.110 | .022 | 7.110 | .681 |
| | TRIALS_10 | 2.3E-03 | 1 | 2.3E-03 | .236 | .637 | .236 | .073 |
| | TRIALS_11 | 2.5E-03 | 1 | 2.5E-03 | .386 | .547 | .386 | .088 |
| Error(TRIALS) | TRIALS_1 | .496 | 11 | 4.5E-02 | | | | |
| | TRIALS_2 | 8.9E-02 | 11 | 8.1E-03 | | | | |
| | TRIALS_3 | .137 | 11 | 1.2E-02 | | | | |
| | TRIALS_4 | 2.4E-02 | 11 | 2.2E-03 | | | | |
| | TRIALS_5 | 7.7E-02 | 11 | 7.0E-03 | | | | |
| | TRIALS_6 | .117 | 11 | 1.1E-02 | | | | |
| | TRIALS_7 | 9.3E-02 | 11 | 8.5E-03 | | | | |
| | TRIALS_8 | 6.2E-02 | 11 | 5.6E-03 | | | | |
| | TRIALS_9 | 2.8E-02 | 11 | 2.6E-03 | | | | |
| | TRIALS_10 | .106 | 11 | 9.7E-03 | | | | |
| | TRIALS_11 | 7.0E-02 | 11 | 6.4E-03 | | | | |

a. Computed using alpha = .05

## Light x Increment

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| LIGHT | .266 | 11 | 2.4E-02 | 2.204 | .018 | 24.240 | .918 |
| Error(LIGHT) | 1.327 | 121 | 1.1E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| LIGHT | LIGHT_1 | 3.2E-02 | 1 | 3.2E-02 | 5.686 | .036 | 5.686 | .585 |
| | LIGHT_2 | 1.7E-02 | 1 | 1.7E-02 | .398 | .541 | .398 | .089 |
| | LIGHT_3 | 6.5E-03 | 1 | 6.5E-03 | 1.101 | .317 | 1.101 | .160 |
| | LIGHT_4 | 1.1E-02 | 1 | 1.1E-02 | .698 | .421 | .698 | .119 |
| | LIGHT_5 | 4.0E-03 | 1 | 4.0E-03 | .247 | .629 | .247 | .074 |
| | LIGHT_6 | 7.0E-03 | 1 | 7.0E-03 | .344 | .570 | .344 | .084 |
| | LIGHT_7 | 2.1E-02 | 1 | 2.1E-02 | 1.607 | .231 | 1.607 | .213 |
| | LIGHT_8 | 3.0E-04 | 1 | 3.0E-04 | .041 | .843 | .041 | .054 |
| | LIGHT_9 | 1.3E-04 | 1 | 1.3E-04 | .006 | .938 | .006 | .051 |
| | LIGHT_10 | 9.9E-02 | 1 | 9.9E-02 | 5.421 | .040 | 5.421 | .565 |
| | LIGHT_11 | 7.4E-02 | 1 | 7.4E-02 | 1.483 | .249 | 1.483 | .200 |
| Error(LIGHT) | LIGHT_1 | 6.2E-02 | 11 | 5.6E-03 | | | | |
| | LIGHT_2 | .466 | 11 | 4.2E-02 | | | | |
| | LIGHT_3 | 6.5E-02 | 11 | 5.9E-03 | | | | |
| | LIGHT_4 | .170 | 11 | 1.5E-02 | | | | |
| | LIGHT_5 | .180 | 11 | 1.6E-02 | | | | |
| | LIGHT_6 | .224 | 11 | 2.0E-02 | | | | |
| | LIGHT_7 | .143 | 11 | 1.3E-02 | | | | |
| | LIGHT_8 | 8.0E-02 | 11 | 7.3E-03 | | | | |
| | LIGHT_9 | .231 | 11 | 2.1E-02 | | | | |
| | LIGHT_10 | .201 | 11 | 1.8E-02 | | | | |
| | LIGHT_11 | .546 | 11 | 5.0E-02 | | | | |

a. Computed using alpha = .05

## Odor x Increments

### Tests of Within-Subjects Effects

Measure: MEASURE_1

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Sphericity Assumed | | | | | | | |
| TRIALS | .125 | 11 | 1.1E-02 | 1.212 | .286 | 13.335 | .634 |
| Error(TRIALS) | 1.132 | 121 | 9.4E-03 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | 8.5E-03 | 1 | 8.5E-03 | .313 | .587 | .313 | .081 |
| | TRIALS_2 | 4.7E-02 | 1 | 4.7E-02 | 1.546 | .240 | 1.546 | .206 |
| | TRIALS_3 | 2.7E-03 | 1 | 2.7E-03 | .186 | .675 | .186 | .068 |
| | TRIALS_4 | 2.0E-02 | 1 | 2.0E-02 | .740 | .408 | .740 | .123 |
| | TRIALS_5 | 2.7E-02 | 1 | 2.7E-02 | 1.273 | .283 | 1.273 | .178 |
| | TRIALS_6 | 1.2E-03 | 1 | 1.2E-03 | .063 | .806 | .063 | .056 |
| | TRIALS_7 | 9.1E-03 | 1 | 9.1E-03 | .561 | .469 | .561 | .105 |
| | TRIALS_8 | 9.1E-03 | 1 | 9.1E-03 | .563 | .469 | .563 | .106 |
| | TRIALS_9 | 2.6E-02 | 1 | 2.6E-02 | 1.158 | .305 | 1.158 | .166 |
| | TRIALS_10 | 6.8E-04 | 1 | 6.8E-04 | .055 | .818 | .055 | .055 |
| | TRIALS_11 | 4.0E-03 | 1 | 4.0E-03 | .400 | .540 | .400 | .089 |
| Error(TRIALS) | TRIALS_1 | .299 | 11 | 2.7E-02 | | | | |
| | TRIALS_2 | .334 | 11 | 3.0E-02 | | | | |
| | TRIALS_3 | .160 | 11 | 1.5E-02 | | | | |
| | TRIALS_4 | .297 | 11 | 2.7E-02 | | | | |
| | TRIALS_5 | .234 | 11 | 2.1E-02 | | | | |
| | TRIALS_6 | .209 | 11 | 1.9E-02 | | | | |
| | TRIALS_7 | .178 | 11 | 1.6E-02 | | | | |
| | TRIALS_8 | .177 | 11 | 1.6E-02 | | | | |
| | TRIALS_9 | .248 | 11 | 2.3E-02 | | | | |
| | TRIALS_10 | .134 | 11 | 1.2E-02 | | | | |
| | TRIALS_11 | .111 | 11 | 1.0E-02 | | | | |

a. Computed using alpha = .05

## LS Comparison, Light

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| LIGHT | .267 | 11 | 2.4E-02 | 2.761 | .004 | 30.370 | .968 |
| LIGHT * GROUP | .464 | 22 | 2.1E-02 | 2.399 | .002 | 52.781 | .995 |
| Error(LIGHT) | .869 | 99 | 8.8E-03 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| LIGHT | LIGHT_1 | 7.4E-02 | 1 | 7.4E-02 | 2.575 | .143 | 2.575 | .300 |
| | LIGHT_2 | .203 | 1 | .203 | 9.993 | .012 | 9.993 | .803 |
| | LIGHT_3 | 1.7E-02 | 1 | 1.7E-02 | 1.464 | .257 | 1.464 | .192 |
| | LIGHT_4 | 3.6E-02 | 1 | 3.6E-02 | 1.771 | .216 | 1.771 | .222 |
| | LIGHT_5 | .141 | 1 | .141 | 4.876 | .055 | 4.876 | .505 |
| | LIGHT_6 | .105 | 1 | .105 | 4.846 | .055 | 4.846 | .502 |
| | LIGHT_7 | .126 | 1 | .126 | 6.049 | .036 | 6.049 | .592 |
| | LIGHT_8 | .173 | 1 | .173 | 4.682 | .059 | 4.682 | .489 |
| | LIGHT_9 | 6.5E-02 | 1 | 6.5E-02 | 5.093 | .050 | 5.093 | .522 |
| | LIGHT_10 | 6.8E-02 | 1 | 6.8E-02 | 5.959 | .037 | 5.959 | .586 |
| | LIGHT_11 | 1.9E-03 | 1 | 1.9E-03 | .059 | .813 | .059 | .055 |
| LIGHT * GROUP | LIGHT_1 | .289 | 2 | .144 | 5.050 | .034 | 10.100 | .665 |
| | LIGHT_2 | .252 | 2 | .126 | 6.198 | .020 | 12.395 | .757 |
| | LIGHT_3 | .420 | 2 | .210 | 18.232 | .001 | 36.464 | .996 |
| | LIGHT_4 | .152 | 2 | 7.6E-02 | 3.719 | .066 | 7.439 | .528 |
| | LIGHT_5 | .160 | 2 | 8.0E-02 | 2.767 | .116 | 5.533 | .411 |
| | LIGHT_6 | .130 | 2 | 6.5E-02 | 3.020 | .099 | 6.041 | .444 |
| | LIGHT_7 | 8.6E-02 | 2 | 4.3E-02 | 2.074 | .182 | 4.148 | .319 |
| | LIGHT_8 | .123 | 2 | 6.1E-02 | 1.664 | .243 | 3.329 | .263 |
| | LIGHT_9 | .273 | 2 | .137 | 10.780 | .004 | 21.560 | .944 |
| | LIGHT_10 | 4.7E-02 | 2 | 2.3E-02 | 2.072 | .182 | 4.145 | .319 |
| | LIGHT_11 | .176 | 2 | 8.8E-02 | 2.790 | .114 | 5.580 | .414 |
| Error(LIGHT) | LIGHT_1 | .257 | 9 | 2.9E-02 | | | | |
| | LIGHT_2 | .183 | 9 | 2.0E-02 | | | | |
| | LIGHT_3 | .104 | 9 | 1.2E-02 | | | | |
| | LIGHT_4 | .184 | 9 | 2.0E-02 | | | | |
| | LIGHT_5 | .260 | 9 | 2.9E-02 | | | | |
| | LIGHT_6 | .194 | 9 | 2.2E-02 | | | | |
| | LIGHT_7 | .188 | 9 | 2.1E-02 | | | | |
| | LIGHT_8 | .332 | 9 | 3.7E-02 | | | | |
| | LIGHT_9 | .114 | 9 | 1.3E-02 | | | | |
| | LIGHT_10 | .102 | 9 | 1.1E-02 | | | | |
| | LIGHT_11 | .285 | 9 | 3.2E-02 | | | | |

a. Computed using alpha = .05

**Tests of Between-Subjects Effects**

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 1.740 | 1 | 1.740 | 454.900 | .000 | 454.900 | 1.000 |
| GROUP | 8.1E-03 | 2 | 4.0E-03 | 1.057 | .387 | 2.114 | .181 |
| Error | 3.4E-02 | 9 | 3.8E-03 | | | | |

a. Computed using alpha = .05

# LS Comparison, Landmark

**Descriptive Statistics**

| | group | Mean | Std. Deviation | N |
|---|---|---|---|---|
| LANDMA1 | 1stset | .2460 | .1566 | 5 |
| | 2ndset | .3480 | 7.50E-02 | 5 |
| | 3rdset | .2450 | .2475 | 2 |
| | Total | .2883 | .1389 | 12 |
| LANDMA2 | 1stset | .2160 | .1282 | 5 |
| | 2ndset | .3840 | .1299 | 5 |
| | 3rdset | .2850 | 2.12E-02 | 2 |
| | Total | .2975 | .1364 | 12 |
| LANDMA3 | 1stset | .3180 | 6.22E-02 | 5 |
| | 2ndset | .2840 | 9.15E-02 | 5 |
| | 3rdset | .3350 | .2333 | 2 |
| | Total | .3067 | 9.92E-02 | 12 |
| LANDMA4 | 1stset | .2900 | 4.95E-02 | 5 |
| | 2ndset | .2340 | 3.78E-02 | 5 |
| | 3rdset | .3450 | .1626 | 2 |
| | Total | .2758 | 7.46E-02 | 12 |
| LANDMA5 | 1stset | .3220 | .1252 | 5 |
| | 2ndset | .2680 | .1150 | 5 |
| | 3rdset | .4500 | 7.07E-02 | 2 |
| | Total | .3208 | .1235 | 12 |
| LANDMA6 | 1stset | .3900 | 8.37E-02 | 5 |
| | 2ndset | .3280 | 3.77E-02 | 5 |
| | 3rdset | .2800 | 7.07E-02 | 2 |
| | Total | .3458 | 7.30E-02 | 12 |

**Descriptive Statistics**

| | group | Mean | Std. Deviation | N |
|---|---|---|---|---|
| LANDMA7 | 1stset | .3480 | .1028 | 5 |
| | 2ndset | .3060 | .1163 | 5 |
| | 3rdset | .2500 | 7.07E-02 | 2 |
| | Total | .3142 | .1026 | 12 |
| LANDMA8 | 1stset | .4020 | 6.02E-02 | 5 |
| | 2ndset | .3420 | 9.76E-02 | 5 |
| | 3rdset | .2500 | .1131 | 2 |
| | Total | .3517 | 9.49E-02 | 12 |
| LANDMA9 | 1stset | .4040 | 8.44E-02 | 5 |
| | 2ndset | .3640 | 6.50E-02 | 5 |
| | 3rdset | .2800 | .1273 | 2 |
| | Total | .3667 | 8.72E-02 | 12 |
| LANDMA90 | 1stset | .4580 | 5.07E-02 | 5 |
| | 2ndset | .3220 | 8.41E-02 | 5 |
| | 3rdset | .2500 | .1697 | 2 |
| | Total | .3667 | .1153 | 12 |
| LANDMA91 | 1stset | .4920 | .1087 | 5 |
| | 2ndset | .3840 | 7.70E-02 | 5 |
| | 3rdset | .2650 | 2.12E-02 | 2 |
| | Total | .4092 | .1170 | 12 |
| LANDMA92 | 1stset | .5420 | .1352 | 5 |
| | 2ndset | .3580 | 7.16E-02 | 5 |
| | 3rdset | .2300 | 8.49E-02 | 2 |
| | Total | .4133 | .1555 | 12 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| LANDMARK | .120 | 11 | 1.1E-02 | 1.293 | .240 | 14.225 | .660 |
| LANDMARK * GROUP | .463 | 22 | 2.1E-02 | 2.488 | .001 | 54.744 | .996 |
| Error(LANDMARK) | .837 | 99 | 8.5E-03 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| LANDMARK | LANDMARK_1 | 9.4E-02 | 1 | 9.4E-02 | 2.711 | .134 | 2.711 | .313 |
| | LANDMARK_2 | 6.7E-02 | 1 | 6.7E-02 | 2.370 | .158 | 2.370 | .281 |
| | LANDMARK_3 | 4.1E-02 | 1 | 4.1E-02 | 2.064 | .185 | 2.064 | .251 |
| | LANDMARK_4 | 7.6E-02 | 1 | 7.6E-02 | 5.751 | .040 | 5.751 | .571 |
| | LANDMARK_5 | 9.0E-03 | 1 | 9.0E-03 | .252 | .628 | .252 | .074 |
| | LANDMARK_6 | 1.9E-02 | 1 | 1.9E-02 | 1.143 | .313 | 1.143 | .160 |
| | LANDMARK_7 | 5.7E-02 | 1 | 5.7E-02 | 5.309 | .047 | 5.309 | .538 |
| | LANDMARK_8 | 2.1E-02 | 1 | 2.1E-02 | 1.123 | .317 | 1.123 | .158 |
| | LANDMARK_9 | 7.5E-03 | 1 | 7.5E-03 | .543 | .480 | .543 | .101 |
| | LANDMARK_10 | 1.1E-02 | 1 | 1.1E-02 | 1.086 | .324 | 1.086 | .154 |
| | LANDMARK_11 | 1.3E-04 | 1 | 1.3E-04 | .026 | .875 | .026 | .052 |
| LANDMARK * GROUP | LANDMARK_1 | .252 | 2 | .126 | 3.624 | .070 | 7.247 | .517 |
| | LANDMARK_2 | .380 | 2 | .190 | 6.748 | .016 | 13.495 | .794 |
| | LANDMARK_3 | .164 | 2 | 8.2E-02 | 4.083 | .055 | 8.167 | .569 |
| | LANDMARK_4 | .194 | 2 | 9.7E-02 | 7.369 | .013 | 14.738 | .829 |
| | LANDMARK_5 | .277 | 2 | .138 | 3.866 | .061 | 7.732 | .545 |
| | LANDMARK_6 | 7.0E-02 | 2 | 3.5E-02 | 2.076 | .181 | 4.152 | .320 |
| | LANDMARK_7 | 8.4E-02 | 2 | 4.2E-02 | 3.952 | .059 | 7.905 | .554 |
| | LANDMARK_8 | 5.4E-02 | 2 | 2.7E-02 | 1.487 | .277 | 2.975 | .239 |
| | LANDMARK_9 | 7.4E-02 | 2 | 3.7E-02 | 2.700 | .121 | 5.399 | .403 |
| | LANDMARK_10 | 1.6E-02 | 2 | 8.2E-03 | .803 | .478 | 1.606 | .147 |
| | LANDMARK_11 | 1.8E-02 | 2 | 9.1E-03 | 1.759 | .227 | 3.517 | .276 |
| Error(LANDMARK) | LANDMARK_1 | .312 | 9 | 3.5E-02 | | | | |
| | LANDMARK_2 | .253 | 9 | 2.8E-02 | | | | |
| | LANDMARK_3 | .180 | 9 | 2.0E-02 | | | | |
| | LANDMARK_4 | .118 | 9 | 1.3E-02 | | | | |
| | LANDMARK_5 | .322 | 9 | 3.6E-02 | | | | |
| | LANDMARK_6 | .152 | 9 | 1.7E-02 | | | | |
| | LANDMARK_7 | 9.6E-02 | 9 | 1.1E-02 | | | | |
| | LANDMARK_8 | .165 | 9 | 1.8E-02 | | | | |
| | LANDMARK_9 | .124 | 9 | 1.4E-02 | | | | |
| | LANDMARK_10 | 9.2E-02 | 9 | 1.0E-02 | | | | |
| | LANDMARK_11 | 4.6E-02 | 9 | 5.2E-03 | | | | |

a. Computed using alpha = .05

### Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 1.077 | 1 | 1.077 | 463.551 | .000 | 463.551 | 1.000 |
| GROUP | 1.0E-02 | 2 | 5.1E-03 | 2.212 | .165 | 4.424 | .338 |
| Error | 2.1E-02 | 9 | 2.3E-03 | | | | |

a. Computed using alpha = .05

## LS Comparison, Odor

**Descriptive Statistics**

| | group | Mean | Std. Deviation | N |
|---|---|---|---|---|
| ODOR1 | 1stset | .3900 | 1.00E-02 | 3 |
| | 2ndset | .2900 | 7.94E-02 | 3 |
| | 3rdset | .3883 | .1221 | 6 |
| | Total | .3642 | 9.97E-02 | 12 |
| ODOR2 | 1stset | .2367 | .2122 | 3 |
| | 2ndset | .4167 | 7.23E-02 | 3 |
| | 3rdset | .3483 | 8.33E-02 | 6 |
| | Total | .3375 | .1298 | 12 |
| ODOR3 | 1stset | .2967 | 8.74E-02 | 3 |
| | 2ndset | .3867 | .1206 | 3 |
| | 3rdset | .5117 | .1074 | 6 |
| | Total | .4267 | .1351 | 12 |
| ODOR4 | 1stset | .3667 | 3.51E-02 | 3 |
| | 2ndset | .2733 | .1168 | 3 |
| | 3rdset | .4317 | 6.05E-02 | 6 |
| | Total | .3758 | 9.46E-02 | 12 |
| ODOR5 | 1stset | .3167 | .1185 | 3 |
| | 2ndset | .3967 | .1422 | 3 |
| | 3rdset | .2900 | 3.35E-02 | 6 |
| | Total | .3233 | 9.39E-02 | 12 |
| ODOR6 | 1stset | .3167 | .1361 | 3 |
| | 2ndset | .2400 | 9.00E-02 | 3 |
| | 3rdset | .3550 | 7.58E-02 | 6 |
| | Total | .3167 | 9.93E-02 | 12 |

**Descriptive Statistics**

| | group | Mean | Std. Deviation | N |
|---|---|---|---|---|
| ODOR7 | 1stset | .4100 | 8.54E-02 | 3 |
| | 2ndset | .3067 | 7.09E-02 | 3 |
| | 3rdset | .3500 | 9.14E-02 | 6 |
| | Total | .3542 | 8.67E-02 | 12 |
| ODOR8 | 1stset | .3900 | 8.72E-02 | 3 |
| | 2ndset | .2967 | .1106 | 3 |
| | 3rdset | .3300 | 3.74E-02 | 6 |
| | Total | .3367 | 7.40E-02 | 12 |
| ODOR9 | 1stset | .3233 | .1650 | 3 |
| | 2ndset | .3200 | 9.54E-02 | 3 |
| | 3rdset | .3517 | 5.95E-02 | 6 |
| | Total | .3367 | 9.20E-02 | 12 |
| ODOR90 | 1stset | .3767 | 8.02E-02 | 3 |
| | 2ndset | .2767 | .1747 | 3 |
| | 3rdset | .3083 | 7.39E-02 | 6 |
| | Total | .3175 | .1032 | 12 |
| ODOR91 | 1stset | .3700 | 2.00E-02 | 3 |
| | 2ndset | .3367 | 8.39E-02 | 3 |
| | 3rdset | .3600 | 6.63E-02 | 6 |
| | Total | .3567 | 5.93E-02 | 12 |
| ODOR92 | 1stset | .3100 | 1.73E-02 | 3 |
| | 2ndset | .4000 | 8.89E-02 | 3 |
| | 3rdset | .3400 | 8.05E-02 | 6 |
| | Total | .3475 | 7.48E-02 | 12 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1

Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| ODOR | 6.6E-02 | 11 | 6.0E-03 | .727 | .710 | 7.998 | .378 |
| ODOR * GROUP | .301 | 22 | 1.4E-02 | 1.661 | .048 | 36.546 | .945 |
| Error(ODOR) | .816 | 99 | 8.2E-03 | | | | |

a. Computed using alpha = .05

**Tests of Between-Subjects Effects**

Measure: MEASURE_1

Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 1.283 | 1 | 1.283 | 1340.118 | .000 | 1340.118 | 1.000 |
| GROUP | 2.7E-03 | 2 | 1.4E-03 | 1.428 | .289 | 2.855 | .231 |
| Error | 8.6E-03 | 9 | 9.6E-04 | | | | |

a. Computed using alpha = .05

## Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| ODOR | ODOR_1 | 4.0E-04 | 1 | 4.0E-04 | .080 | .784 | .080 | .057 |
| | ODOR_2 | 2.8E-03 | 1 | 2.8E-03 | .196 | .668 | .196 | .068 |
| | ODOR_3 | 2.5E-02 | 1 | 2.5E-02 | .991 | .345 | .991 | .145 |
| | ODOR_4 | 5.6E-04 | 1 | 5.6E-04 | .041 | .844 | .041 | .054 |
| | ODOR_5 | 2.6E-03 | 1 | 2.6E-03 | .144 | .713 | .144 | .063 |
| | ODOR_6 | 2.3E-02 | 1 | 2.3E-02 | 1.331 | .278 | 1.331 | .179 |
| | ODOR_7 | 3.3E-04 | 1 | 3.3E-04 | .033 | .859 | .033 | .053 |
| | ODOR_8 | 1.3E-03 | 1 | 1.3E-03 | .118 | .739 | .118 | .061 |
| | ODOR_9 | 3.6E-03 | 1 | 3.6E-03 | .236 | .639 | .236 | .072 |
| | ODOR_10 | 9.4E-03 | 1 | 9.4E-03 | .431 | .528 | .431 | .091 |
| | ODOR_11 | 3.3E-04 | 1 | 3.3E-04 | .022 | .884 | .022 | .052 |
| ODOR * GROUP | ODOR_1 | 6.6E-02 | 2 | 3.3E-02 | 6.548 | .018 | 13.096 | .781 |
| | ODOR_2 | 1.6E-02 | 2 | 8.1E-03 | .567 | .586 | 1.134 | .117 |
| | ODOR_3 | .103 | 2 | 5.1E-02 | 2.017 | .189 | 4.035 | .312 |
| | ODOR_4 | 9.9E-02 | 2 | 4.9E-02 | 3.599 | .071 | 7.198 | .514 |
| | ODOR_5 | 8.2E-03 | 2 | 4.1E-03 | .224 | .803 | .449 | .075 |
| | ODOR_6 | 6.7E-02 | 2 | 3.3E-02 | 1.939 | .199 | 3.878 | .301 |
| | ODOR_7 | 5.6E-02 | 2 | 2.8E-02 | 2.808 | .113 | 5.616 | .417 |
| | ODOR_8 | 5.0E-02 | 2 | 2.5E-02 | 2.236 | .163 | 4.473 | .341 |
| | ODOR_9 | 1.9E-02 | 2 | 9.6E-03 | .622 | .559 | 1.243 | .124 |
| | ODOR_10 | 5.4E-02 | 2 | 2.7E-02 | 1.246 | .333 | 2.493 | .206 |
| | ODOR_11 | 2.4E-02 | 2 | 1.2E-02 | .817 | .472 | 1.634 | .149 |
| Error(ODOR) | ODOR_1 | 4.5E-02 | 9 | 5.1E-03 | | | | |
| | ODOR_2 | .128 | 9 | 1.4E-02 | | | | |
| | ODOR_3 | .229 | 9 | 2.5E-02 | | | | |
| | ODOR_4 | .123 | 9 | 1.4E-02 | | | | |
| | ODOR_5 | .164 | 9 | 1.8E-02 | | | | |
| | ODOR_6 | .155 | 9 | 1.7E-02 | | | | |
| | ODOR_7 | 9.0E-02 | 9 | 1.0E-02 | | | | |
| | ODOR_8 | .101 | 9 | 1.1E-02 | | | | |
| | ODOR_9 | .139 | 9 | 1.5E-02 | | | | |
| | ODOR_10 | .196 | 9 | 2.2E-02 | | | | |
| | ODOR_11 | .133 | 9 | 1.5E-02 | | | | |

a. Computed using alpha = .05

## Cue x Increment, LS1

**Descriptive Statistics**

|  | cue | Mean | Std. Deviation | N |
|---|---|---|---|---|
| TRIAL1 | landmark | .2460 | .1566 | 5 |
|  | light | .3150 | 9.75E-02 | 4 |
|  | odor | .3900 | 1.00E-02 | 3 |
|  | Total | .3050 | .1230 | 12 |
| TRIAL2 | landmark | .2160 | .1282 | 5 |
|  | light | .2875 | 3.50E-02 | 4 |
|  | odor | .2367 | .2122 | 3 |
|  | Total | .2450 | .1247 | 12 |
| TRIAL3 | landmark | .3180 | 6.22E-02 | 5 |
|  | light | .3300 | .2112 | 4 |
|  | odor | .2967 | 8.74E-02 | 3 |
|  | Total | .3167 | .1230 | 12 |
| TRIAL4 | landmark | .2900 | 4.95E-02 | 5 |
|  | light | .3925 | 6.40E-02 | 4 |
|  | odor | .3667 | 3.51E-02 | 3 |
|  | Total | .3433 | 6.75E-02 | 12 |
| TRIAL5 | landmark | .3220 | .1252 | 5 |
|  | light | .3375 | 6.18E-02 | 4 |
|  | odor | .3167 | .1185 | 3 |
|  | Total | .3258 | 9.68E-02 | 12 |
| TRIAL6 | landmark | .3900 | 8.37E-02 | 5 |
|  | light | .3875 | 5.56E-02 | 4 |
|  | odor | .3167 | .1361 | 3 |
|  | Total | .3708 | 8.85E-02 | 12 |
| TRIAL7 | landmark | .3480 | .1028 | 5 |
|  | light | .3900 | 6.16E-02 | 4 |
|  | odor | .4100 | 8.54E-02 | 3 |
|  | Total | .3775 | 8.34E-02 | 12 |
| TRIAL8 | landmark | .4020 | 6.02E-02 | 5 |
|  | light | .3575 | .1668 | 4 |
|  | odor | .3900 | 8.72E-02 | 3 |
|  | Total | .3842 | .1034 | 12 |
| TRIAL9 | landmark | .4040 | 8.44E-02 | 5 |
| TRIAL9 | light | .3275 | .1072 | 4 |
|  | odor | .3233 | .1650 | 3 |
|  | Total | .3583 | .1109 | 12 |
| TRIAL10 | landmark | .4580 | 5.07E-02 | 5 |
|  | light | .4425 | 2.75E-02 | 4 |
|  | odor | .3767 | 8.02E-02 | 3 |
|  | Total | .4325 | 5.91E-02 | 12 |
| TRIAL11 | landmark | .4920 | .1087 | 5 |
|  | light | .4600 | 5.72E-02 | 4 |
|  | odor | .3700 | 2.00E-02 | 3 |
|  | Total | .4508 | 8.86E-02 | 12 |
| TRIAL12 | landmark | .5420 | .1352 | 5 |
|  | light | .6050 | .1524 | 4 |
|  | odor | .3100 | 1.73E-02 | 3 |
|  | Total | .5050 | .1663 | 12 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1

Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| TRIALS | .522 | 11 | 4.7E-02 | 4.707 | .000 | 51.781 | 1.000 |
| TRIALS * CUE | .284 | 22 | 1.3E-02 | 1.281 | .203 | 28.193 | .850 |
| Error(TRIALS) | .997 | 99 | 1.0E-02 |  |  |  |  |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | 5.7E-02 | 1 | 5.7E-02 | 3.681 | .087 | 3.681 | .403 |
| TRIALS | TRIALS_2 | 5.1E-05 | 1 | 5.1E-05 | .002 | .970 | .002 | .050 |
| | TRIALS_3 | 1.2E-02 | 1 | 1.2E-02 | 1.558 | .243 | 1.558 | .201 |
| | TRIALS_4 | 8.1E-04 | 1 | 8.1E-04 | .024 | .881 | .024 | .052 |
| | TRIALS_5 | 2.6E-02 | 1 | 2.6E-02 | 1.559 | .243 | 1.559 | .201 |
| | TRIALS_6 | 5.0E-02 | 1 | 5.0E-02 | 2.364 | .159 | 2.364 | .280 |
| | TRIALS_7 | 5.0E-02 | 1 | 5.0E-02 | 5.508 | .044 | 5.508 | .553 |
| | TRIALS_8 | 1.4E-02 | 1 | 1.4E-02 | .655 | .439 | .655 | .112 |
| | TRIALS_9 | .136 | 1 | .136 | 6.439 | .032 | 6.439 | .619 |
| | TRIALS_10 | .176 | 1 | .176 | 6.475 | .031 | 6.475 | .621 |
| | TRIALS_11 | .327 | 1 | .327 | 8.312 | .018 | 8.312 | .728 |
| TRIALS * CUE | TRIALS_1 | 3.5E-02 | 2 | 1.7E-02 | 1.131 | .365 | 2.261 | .191 |
| | TRIALS_2 | 5.1E-02 | 2 | 2.6E-02 | .754 | .498 | 1.507 | .141 |
| | TRIALS_3 | 1.8E-02 | 2 | 8.9E-03 | 1.121 | .367 | 2.242 | .189 |
| | TRIALS_4 | 4.2E-02 | 2 | 2.1E-02 | .614 | .562 | 1.228 | .123 |
| | TRIALS_5 | 8.9E-02 | 2 | 4.4E-02 | 2.646 | .125 | 5.292 | .396 |
| | TRIALS_6 | 1.3E-02 | 2 | 6.3E-03 | .302 | .747 | .603 | .085 |
| | TRIALS_7 | 5.4E-02 | 2 | 2.7E-02 | 2.940 | .104 | 5.880 | .433 |
| | TRIALS_8 | .105 | 2 | 5.2E-02 | 2.489 | .138 | 4.977 | .375 |
| | TRIALS_9 | 9.5E-02 | 2 | 4.8E-02 | 2.257 | .161 | 4.514 | .344 |
| | TRIALS_10 | .133 | 2 | 6.6E-02 | 2.445 | .142 | 4.889 | .369 |
| | TRIALS_11 | .314 | 2 | .157 | 3.988 | .058 | 7.977 | .558 |
| Error(TRIALS) | TRIALS_1 | .139 | 9 | 1.5E-02 | | | | |
| | TRIALS_2 | .306 | 9 | 3.4E-02 | | | | |
| | TRIALS_3 | 7.1E-02 | 9 | 7.9E-03 | | | | |
| | TRIALS_4 | .306 | 9 | 3.4E-02 | | | | |
| | TRIALS_5 | .151 | 9 | 1.7E-02 | | | | |
| | TRIALS_6 | .189 | 9 | 2.1E-02 | | | | |
| | TRIALS_7 | 8.2E-02 | 9 | 9.1E-03 | | | | |
| | TRIALS_8 | .189 | 9 | 2.1E-02 | | | | |
| | TRIALS_9 | .190 | 9 | 2.1E-02 | | | | |
| | TRIALS_10 | .244 | 9 | 2.7E-02 | | | | |
| | TRIALS_11 | .354 | 9 | 3.9E-02 | | | | |

### Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 1.536 | 1 | 1.536 | 920.194 | .000 | 920.194 | 1.000 |
| CUE | 3.3E-03 | 2 | 1.7E-03 | 1.001 | .405 | 2.003 | .173 |
| Error | 1.5E-02 | 9 | 1.7E-03 | | | | |

a. Computed using alpha = .05

# Light x Increments, LS 1

**Tests of Within-Subjects Effects**

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| TRIALS | .325 | 11 | 3.0E-02 | 2.899 | .009 | 31.887 | .940 |
| Error(TRIALS) | .336 | 33 | 1.0E-02 | | | | |

a. Computed using alpha = .05

**Tests of Within-Subjects Contrasts**

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | 3.0E-03 | 1 | 3.0E-03 | .245 | .655 | .245 | .065 |
| | TRIALS_2 | 9.0E-04 | 1 | 9.0E-04 | .016 | .907 | .016 | .051 |
| | TRIALS_3 | 2.4E-02 | 1 | 2.4E-02 | 7.299 | .074 | 7.299 | .458 |
| | TRIALS_4 | 2.0E-03 | 1 | 2.0E-03 | .093 | .781 | .093 | .056 |
| | TRIALS_5 | 2.1E-02 | 1 | 2.1E-02 | .938 | .404 | .938 | .107 |
| | TRIALS_6 | 2.2E-02 | 1 | 2.2E-02 | .952 | .401 | .952 | .108 |
| | TRIALS_7 | 7.2E-03 | 1 | 7.2E-03 | .923 | .407 | .923 | .107 |
| | TRIALS_8 | 6.3E-04 | 1 | 6.3E-04 | .064 | .817 | .064 | .054 |
| | TRIALS_9 | 6.5E-02 | 1 | 6.5E-02 | 6.618 | .082 | 6.618 | .426 |
| | TRIALS_10 | 8.4E-02 | 1 | 8.4E-02 | 7.229 | .074 | 7.229 | .455 |
| | TRIALS_11 | .336 | 1 | .336 | 11.139 | .044 | 11.139 | .614 |
| Error(TRIALS) | TRIALS_1 | 3.7E-02 | 3 | 1.2E-02 | | | | |
| | TRIALS_2 | .168 | 3 | 5.6E-02 | | | | |
| | TRIALS_3 | 9.9E-03 | 3 | 3.3E-03 | | | | |
| | TRIALS_4 | 6.5E-02 | 3 | 2.2E-02 | | | | |
| | TRIALS_5 | 6.7E-02 | 3 | 2.2E-02 | | | | |
| | TRIALS_6 | 7.1E-02 | 3 | 2.4E-02 | | | | |
| | TRIALS_7 | 2.3E-02 | 3 | 7.8E-03 | | | | |
| | TRIALS_8 | 2.9E-02 | 3 | 9.8E-03 | | | | |
| | TRIALS_9 | 2.9E-02 | 3 | 9.8E-03 | | | | |
| | TRIALS_10 | 3.5E-02 | 3 | 1.2E-02 | | | | |
| | TRIALS_11 | 9.1E-02 | 3 | 3.0E-02 | | | | |

a. Computed using alpha = .05

## Landmark x Increments, LS 1

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| TRIALS | .529 | 11 | 4.8E-02 | 4.721 | .000 | 51.926 | .998 |
| Error(TRIALS) | .448 | 44 | 1.0E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | 4.5E-03 | 1 | 4.5E-03 | 3.333 | .142 | 3.333 | .290 |
| | TRIALS_2 | 2.6E-02 | 1 | 2.6E-02 | .871 | .404 | .871 | .113 |
| | TRIALS_3 | 9.7E-03 | 1 | 9.7E-03 | .671 | .459 | .671 | .098 |
| | TRIALS_4 | 2.9E-02 | 1 | 2.9E-02 | .543 | .502 | .543 | .089 |
| | TRIALS_5 | .104 | 1 | .104 | 10.037 | .034 | 10.037 | .664 |
| | TRIALS_6 | 5.2E-02 | 1 | 5.2E-02 | 2.050 | .225 | 2.050 | .199 |
| | TRIALS_7 | .122 | 1 | .122 | 10.463 | .032 | 10.463 | .681 |
| | TRIALS_8 | .125 | 1 | .125 | 5.060 | .088 | 5.060 | .405 |
| | TRIALS_9 | .225 | 1 | .225 | 6.239 | .067 | 6.239 | .477 |
| | TRIALS_10 | .303 | 1 | .303 | 5.799 | .074 | 5.799 | .451 |
| | TRIALS_11 | .438 | 1 | .438 | 6.690 | .061 | 6.690 | .502 |
| Error(TRIALS) | TRIALS_1 | 5.4E-03 | 4 | 1.4E-03 | | | | |
| | TRIALS_2 | .119 | 4 | 3.0E-02 | | | | |
| | TRIALS_3 | 5.8E-02 | 4 | 1.4E-02 | | | | |
| | TRIALS_4 | .213 | 4 | 5.3E-02 | | | | |
| | TRIALS_5 | 4.1E-02 | 4 | 1.0E-02 | | | | |
| | TRIALS_6 | .101 | 4 | 2.5E-02 | | | | |
| | TRIALS_7 | 4.7E-02 | 4 | 1.2E-02 | | | | |
| | TRIALS_8 | 9.9E-02 | 4 | 2.5E-02 | | | | |
| | TRIALS_9 | .144 | 4 | 3.6E-02 | | | | |
| | TRIALS_10 | .209 | 4 | 5.2E-02 | | | | |
| | TRIALS_11 | .262 | 4 | 6.5E-02 | | | | |

a. Computed using alpha = .05

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| subject | cuegrp | bcr1 | bcl1 | bcm1 | bco1 |
|---|---|---|---|---|---|
| 1 | light | .27 | .54 | .17 | .02 |
| 2 | land | .22 | .49 | .29 | .00 |
| 3 | land | .44 | .36 | .17 | .03 |
| 4 | odor | .44 | .18 | .23 | .15 |
| 5 | land | .26 | .50 | .23 | .01 |
| 6 | land | .31 | .42 | .24 | .03 |
| 7 | land | .34 | .41 | .19 | .06 |
| 8 | light | .24 | .47 | .24 | .05 |
| 9 | odor | .25 | .49 | .24 | .03 |
| 13 | light | .17 | .57 | .22 | .04 |
| 15 | light | .67 | .11 | .07 | .14 |
| 16 | odor | .54 | .36 | .09 | .01 |
| . | . | . | . | . | . |

1-1

# Odor x Increments, LS 1

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power$^a$ |
|---|---|---|---|---|---|---|---|
| TRIALS | 8.3E-02 | 11 | 7.5E-03 | .778 | .658 | 8.556 | .301 |
| Error(TRIALS) | .213 | 22 | 9.7E-03 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power$^a$ |
|---|---|---|---|---|---|---|---|---|
| TRIALS | TRIALS_1 | 7.1E-02 | 1 | 7.1E-02 | 1.465 | .350 | 1.465 | .115 |
| | TRIALS_2 | 2.6E-02 | 1 | 2.6E-02 | 2.770 | .238 | 2.770 | .170 |
| | TRIALS_3 | 1.6E-03 | 1 | 1.6E-03 | .942 | .434 | .942 | .093 |
| | TRIALS_4 | 1.6E-02 | 1 | 1.6E-02 | 1.150 | .396 | 1.150 | .102 |
| | TRIALS_5 | 1.6E-02 | 1 | 1.6E-02 | .760 | .475 | .760 | .085 |
| | TRIALS_6 | 1.2E-03 | 1 | 1.2E-03 | .148 | .737 | .148 | .057 |
| | TRIALS_7 | .000 | 1 | .000 | .000 | 1.000 | .000 | .050 |
| | TRIALS_8 | 1.3E-02 | 1 | 1.3E-02 | .437 | .577 | .437 | .070 |
| | TRIALS_9 | 5.3E-04 | 1 | 5.3E-04 | .066 | .822 | .066 | .053 |
| | TRIALS_10 | 1.2E-03 | 1 | 1.2E-03 | 4.000 | .184 | 4.000 | .218 |
| | TRIALS_11 | 1.9E-02 | 1 | 1.9E-02 | 27.429 | .035 | 27.429 | .751 |
| Error(TRIALS) | TRIALS_1 | 9.6E-02 | 2 | 4.8E-02 | | | | |
| | TRIALS_2 | 1.9E-02 | 2 | 9.4E-03 | | | | |
| | TRIALS_3 | 3.5E-03 | 2 | 1.7E-03 | | | | |
| | TRIALS_4 | 2.8E-02 | 2 | 1.4E-02 | | | | |
| | TRIALS_5 | 4.2E-02 | 2 | 2.1E-02 | | | | |
| | TRIALS_6 | 1.6E-02 | 2 | 8.1E-03 | | | | |
| | TRIALS_7 | 1.2E-02 | 2 | 6.1E-03 | | | | |
| | TRIALS_8 | 6.1E-02 | 2 | 3.1E-02 | | | | |
| | TRIALS_9 | 1.6E-02 | 2 | 8.1E-03 | | | | |
| | TRIALS_10 | 6.0E-04 | 2 | 3.0E-04 | | | | |
| | TRIALS_11 | 1.4E-03 | 2 | 7.0E-04 | | | | |

a. Computed using alpha = .05

## Goalbox Position, LS 1

### Descriptive Statistics

|  | cuegrp | Mean | Std. Deviation | N |
|---|---|---|---|---|
| BCL1 | land | .4360 | 5.86E-02 | 5 |
|  | light | .4225 | .2125 | 4 |
|  | odor | .3433 | .1557 | 3 |
|  | Total | .4083 | .1398 | 12 |
| BCM1 | land | .2240 | 4.67E-02 | 5 |
|  | light | .1750 | 7.59E-02 | 4 |
|  | odor | .1867 | 8.39E-02 | 3 |
|  | Total | .1983 | 6.46E-02 | 12 |
| BCR1 | land | .3140 | 8.41E-02 | 5 |
|  | light | .3375 | .2256 | 4 |
|  | odor | .4100 | .1473 | 3 |
|  | Total | .3458 | .1484 | 12 |

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| FACTOR1 | .266 | 2 | .133 | 5.279 | .016 | 10.558 | .766 |
| FACTOR1 * CUEGRP | 4.0E-02 | 4 | 9.9E-03 | .392 | .812 | 1.568 | .120 |
| Error(FACTOR1) | .454 | 18 | 2.5E-02 |  |  |  |  |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| FACTOR1 | FACTOR1_1 | 1.3E-02 | 1 | 1.3E-02 | .285 | .606 | .285 | .077 |
|  | FACTOR1_2 | .254 | 1 | .254 | 40.145 | .000 | 40.145 | 1.000 |
| FACTOR1 * CUEGRP | FACTOR1_1 | 3.5E-02 | 2 | 1.7E-02 | .395 | .685 | .791 | .096 |
|  | FACTOR1_2 | 4.7E-03 | 2 | 2.3E-03 | .368 | .702 | .737 | .093 |
| Error(FACTOR1) | FACTOR1_1 | .397 | 9 | 4.4E-02 |  |  |  |  |
|  | FACTOR1_2 | 5.7E-02 | 9 | 6.3E-03 |  |  |  |  |

a. Computed using alpha = .05

### Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 3.454 | 1 | 3.454 | 3818.872 | .000 | 3818.872 | 1.000 |
| CUEGRP | 1.3E-03 | 2 | 6.7E-04 | .738 | .505 | 1.476 | .139 |
| Error | 8.1E-03 | 9 | 9.0E-04 |  |  |  |  |

a. Computed using alpha = .05

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|  | cue2 | bcr2 | bcl2 | bcm2 | bco2 |
|---|---|---|---|---|---|
| 1 | land | .27 | .53 | .20 | .00 |
| 2 | odor | .09 | .56 | .35 | .00 |
| 3 | light | .55 | .10 | .35 | .00 |
| 4 | light | .31 | .31 | .37 | .00 |
| 5 | light | .22 | .48 | .23 | .07 |
| 6 | light | .25 | .34 | .40 | .01 |
| 7 | odor | .44 | .24 | .16 | .16 |
| 8 | land | .31 | .36 | .30 | .03 |
| 9 | land | .34 | .48 | .18 | .00 |
| 10 | land | .30 | .34 | .31 | .07 |
| 11 | light | .71 | .05 | .15 | .08 |
| 12 | land | .21 | .58 | .07 | .03 |
| 13 | . | . | . | . | . |

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# Goalbox Position, LS 2

**Descriptive Statistics**

| | cuegrp | Mean | Std. Deviation | N |
|---|---|---|---|---|
| BCL2 | land | .3440 | .1841 | 5 |
| | light | .3200 | .1992 | 4 |
| | odor | .4567 | .1365 | 3 |
| | Total | .3642 | .1725 | 12 |
| BCM2 | land | .2980 | 9.93E-02 | 5 |
| | light | .2400 | 7.79E-02 | 4 |
| | odor | .2067 | .1518 | 3 |
| | Total | .2558 | .1048 | 12 |
| BCR2 | land | .3100 | .1834 | 5 |
| | light | .3975 | .2090 | 4 |
| | odor | .2867 | 6.81E-02 | 3 |
| | Total | .3333 | .1653 | 12 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| FACTOR1 | 9.3E-02 | 2 | 4.7E-02 | 1.277 | .303 | 2.554 | .241 |
| FACTOR1 * CUEGRP | 7.8E-02 | 4 | 2.0E-02 | .535 | .712 | 2.141 | .149 |
| Error(FACTOR1) | .659 | 18 | 3.7E-02 | | | | |

a. Computed using alpha = .05

**Tests of Within-Subjects Contrasts**

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| FACTOR1 | FACTOR1_1 | 1.0E-02 | 1 | 1.0E-02 | .169 | .690 | .169 | .066 |
| | FACTOR1_2 | 8.3E-02 | 1 | 8.3E-02 | 6.491 | .031 | 6.491 | .622 |
| FACTOR1 * CUEGRP | FACTOR1_1 | 5.3E-02 | 2 | 2.6E-02 | .435 | .660 | .871 | .101 |
| | FACTOR1_2 | 2.6E-02 | 2 | 1.3E-02 | 1.005 | .404 | 2.011 | .174 |
| Error(FACTOR1) | FACTOR1_1 | .543 | 9 | 6.0E-02 | | | | |
| | FACTOR1_2 | .115 | 9 | 1.3E-02 | | | | |

a. Computed using alpha = .05

**Tests of Between-Subjects Effects**

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 3.479 | 1 | 3.479 | 2642.259 | .000 | 2642.259 | 1.000 |
| CUEGRP | 3.7E-05 | 2 | 1.9E-05 | .014 | .986 | .028 | .052 |
| Error | 1.2E-02 | 9 | 1.3E-03 | | | | |

a. Computed using alpha = .05

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| | cue3 | bcr3 | bcl3 | bcm3 | bco3 |
|---|---|---|---|---|---|
| 1 | odor | .56 | .37 | .31 | .00 |
| 2 | light | .14 | .49 | .37 | .00 |
| 3 | odor | .41 | .28 | .31 | .00 |
| 4 | land | .37 | .32 | .16 | .15 |
| 5 | odor | .70 | .08 | .18 | .04 |
| 6 | odor | .24 | .43 | .32 | .00 |
| 7 | light | .40 | .36 | .19 | .05 |
| 8 | odor | .15 | .55 | .28 | .02 |
| 9 | light | .41 | .30 | .26 | .03 |
| 10 | odor | .23 | .34 | .41 | .02 |
| 11 | land | .73 | .09 | .16 | .01 |
| 12 | light | .29 | .63 | .08 | .00 |

# Goalbox Position, LS 3

### Descriptive Statistics

| | cuegrp | Mean | Std. Deviation | N |
|---|---|---|---|---|
| BCL3 | land | .3280 | .1593 | 5 |
| | light | .3375 | .1893 | 4 |
| | odor | .4167 | .1850 | 3 |
| | Total | .3533 | .1634 | 12 |
| BCM3 | land | .2740 | 8.44E-02 | 5 |
| | light | .2900 | .1030 | 4 |
| | odor | .1667 | 9.02E-02 | 3 |
| | Total | .2525 | 9.85E-02 | 12 |
| BCR3 | land | .3780 | .2126 | 5 |
| | light | .4175 | .2737 | 4 |
| | odor | .3567 | 6.11E-02 | 3 |
| | Total | .3858 | .1954 | 12 |

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| FACTOR1 | .130 | 2 | 6.5E-02 | 1.573 | .235 | 3.146 | .289 |
| FACTOR1 * CUEGRP | 4.6E-02 | 4 | 1.2E-02 | .281 | .887 | 1.122 | .098 |
| Error(FACTOR1) | .745 | 18 | 4.1E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| FACTOR1 | FACTOR1_1 | 3.1E-03 | 1 | 3.1E-03 | .045 | .837 | .045 | .054 |
| | FACTOR1_2 | .127 | 1 | .127 | 9.959 | .012 | 9.959 | .801 |
| FACTOR1 * CUEGRP | FACTOR1_1 | 1.8E-02 | 2 | 9.1E-03 | .129 | .880 | .259 | .064 |
| | FACTOR1_2 | 2.8E-02 | 2 | 1.4E-02 | 1.110 | .371 | 2.221 | .188 |
| Error(FACTOR1) | FACTOR1_1 | .630 | 9 | 7.0E-02 | | | | |
| | FACTOR1_2 | .115 | 9 | 1.3E-02 | | | | |

a. Computed using alpha = .05

### Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 3.741 | 1 | 3.741 | 1542.070 | .000 | 1542.070 | 1.000 |
| CUEGRP | 6.7E-03 | 2 | 3.3E-03 | 1.379 | .300 | 2.757 | .224 |
| Error | 2.2E-02 | 9 | 2.4E-03 | | | | |

a. Computed using alpha = .05

## Experiment 2

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| | age | landmark | light | odor | nocue |
|---|---|---|---|---|---|
| 1 | 3 yrs | .19 | .37 | .30 | .14 |
| 2 | 3 yrs | .26 | .26 | .37 | .11 |
| 3 | 3 yrs | .11 | .44 | .33 | .12 |
| 4 | 3 yrs | .19 | .44 | .26 | .11 |
| 5 | 5 mo | .28 | .28 | .28 | .16 |
| 6 | 5 mo | .17 | .42 | .31 | .10 |
| 7 | 5 mo | .22 | .28 | .31 | .19 |
| 8 | 5 mo | .33 | .31 | .33 | .03 |
| 9 | 1 yr | .33 | .24 | .29 | .14 |
| 10 | 1 yr | .31 | .29 | .24 | .16 |
| 11 | 1 yr | .29 | .20 | .40 | .11 |
| 12 | 1 yr | .20 | .24 | .38 | .18 |

## Cue Choice

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| CUES | 4.6E-02 | 2 | 2.3E-02 | 3.358 | .053 | 6.715 | .573 |
| Error(CUES) | .149 | 22 | 6.8E-03 | | | | |

a. Computed using alpha = .05

simple contrast to first: landmark to light, landmark to odor

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUES | CUES_1 | 6.6E-02 | 1 | 6.6E-02 | 3.263 | .098 | 3.263 | .378 |
| | CUES_2 | 7.1E-02 | 1 | 7.1E-02 | 9.057 | .012 | 9.057 | .782 |
| Error(CUES) | CUES_1 | .222 | 11 | 2.0E-02 | | | | |
| | CUES_2 | 8.6E-02 | 11 | 7.8E-03 | | | | |

a. Computed using alpha = .05

simple contrast to last: odor to landmark, odor to light

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUES | CUES_1 | 7.1E-02 | 1 | 7.1E-02 | 9.057 | .012 | 9.057 | .782 |
| | CUES_2 | 7.5E-05 | 1 | 7.5E-05 | .006 | .940 | .006 | .051 |
| Error(CUES) | CUES_1 | 8.6E-02 | 11 | 7.8E-03 | | | | |
| | CUES_2 | .139 | 11 | 1.3E-02 | | | | |

a. Computed using alpha = .05

## Cue Choice x Age

### Descriptive Statistics

| | Age | Mean | Std. Deviation | N |
|---|---|---|---|---|
| LANDMARK | 5 mo | .2500 | 6.98E-02 | 4 |
| | 1 yr | .2825 | 5.74E-02 | 4 |
| | 3 yrs | .1875 | 6.13E-02 | 4 |
| | Total | .2400 | 7.03E-02 | 12 |
| LIGHT | 5 mo | .3225 | 6.65E-02 | 4 |
| | 1 yr | .2425 | 3.69E-02 | 4 |
| | 3 yrs | .3775 | 8.50E-02 | 4 |
| | Total | .3142 | 8.31E-02 | 12 |
| ODOR | 5 mo | .3075 | 2.06E-02 | 4 |
| | 1 yr | .3275 | 7.54E-02 | 4 |
| | 3 yrs | .3150 | 4.65E-02 | 4 |
| | Total | .3167 | 4.83E-02 | 12 |

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| CUES | 4.6E-02 | 2 | 2.3E-02 | 4.382 | .028 | 8.764 | .681 |
| CUES * AGE | 5.6E-02 | 4 | 1.4E-02 | 2.678 | .065 | 10.712 | .622 |
| Error(CUES) | 9.4E-02 | 18 | 5.2E-03 | | | | |

a. Computed using alpha = .05

simple contrast to first: landmark to light , landmark to odor

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUES | CUES_1 | 6.6E-02 | 1 | 6.6E-02 | 5.092 | .050 | 5.092 | .522 |
| | CUES_2 | 7.1E-02 | 1 | 7.1E-02 | 9.088 | .015 | 9.088 | .765 |
| CUES * AGE | CUES_1 | .106 | 2 | 5.3E-02 | 4.081 | .055 | 8.162 | .569 |
| | CUES_2 | 1.6E-02 | 2 | 7.9E-03 | 1.019 | .399 | 2.038 | .176 |
| Error(CUES) | CUES_1 | .117 | 9 | 1.3E-02 | | | | |
| | CUES_2 | 7.0E-02 | 9 | 7.8E-03 | | | | |

a. Computed using alpha = .05

simple contrast to last: odor to landmark, odor to light

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUES | CUES_1 | 7.1E-02 | 1 | 7.1E-02 | 9.088 | .015 | 9.088 | .765 |
| | CUES_2 | 7.5E-05 | 1 | 7.5E-05 | .007 | .934 | .007 | .051 |
| CUES * AGE | CUES_1 | 1.6E-02 | 2 | 7.9E-03 | 1.019 | .399 | 2.038 | .176 |
| | CUES_2 | 4.5E-02 | 2 | 2.3E-02 | 2.169 | .170 | 4.339 | .332 |
| Error(CUES) | CUES_1 | 7.0E-02 | 9 | 7.8E-03 | | | | |
| | CUES_2 | 9.4E-02 | 9 | 1.0E-02 | | | | |

a. Computed using alpha = .05

A:\exp2correctpercent.sav

| | subject | age | landmark | light | odor |
|---|---|---|---|---|---|
| 1 | 1.00 | 1yr | .33 | .42 | .33 |
| 2 | 2.00 | 1yr | .42 | .58 | .50 |
| 3 | 3.00 | 1yr | .50 | .42 | .67 |
| 4 | 4.00 | 1yr | .25 | .25 | .08 |
| 5 | 5.00 | 1yr | .17 | .00 | .33 |
| 6 | 6.00 | 5mo | .33 | .50 | .42 |
| 7 | 7.00 | 5mo | .42 | .17 | .25 |
| 8 | 8.00 | 5mo | .17 | .25 | .25 |
| 9 | 9.00 | 5mo | .42 | .17 | .33 |
| 10 | 13.00 | 3yr | .33 | .33 | .50 |
| 11 | 15.00 | 3yr | .33 | .25 | .25 |
| 12 | 16.00 | 3yr | .33 | .50 | .25 |

## Rewarded Cue Choice, Retraining Trials

**Descriptive Statistics**

| | Mean | Std. Deviation | N |
|---|---|---|---|
| LANDMARK | .3333 | .1003 | 12 |
| LIGHT | .3200 | .1691 | 12 |
| ODOR | .3467 | .1556 | 12 |

**Tests of Within-Subjects Effects**

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| CUE | 4.3E-03 | 2 | 2.1E-03 | .181 | .836 | .361 | .075 |
| Error(CUE) | .260 | 22 | 1.2E-02 | | | | |

a. Computed using alpha = .05

**Tests of Within-Subjects Contrasts**

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUE | CUE_1 | 1.1E-03 | 1 | 1.1E-03 | .130 | .726 | .130 | .063 |
| | CUE_2 | 3.2E-03 | 1 | 3.2E-03 | .208 | .657 | .208 | .070 |
| Error(CUE) | CUE_1 | 9.0E-02 | 11 | 8.2E-03 | | | | |
| | CUE_2 | .169 | 11 | 1.5E-02 | | | | |

a. Computed using alpha = .05

## Rewarded Cue Choice x Age

**Descriptive Statistics**

| | age | Mean | Std. Deviation | N |
|---|---|---|---|---|
| LANDMARK | 5mo | .3350 | .1179 | 4 |
| | 1yr | .3340 | .1313 | 5 |
| | 3yr | .3300 | .0000 | 3 |
| | Total | .3333 | .1003 | 12 |
| LIGHT | 5mo | .2725 | .1563 | 4 |
| | 1yr | .3340 | .2202 | 5 |
| | 3yr | .3600 | .1277 | 3 |
| | Total | .3200 | .1691 | 12 |
| ODOR | 5mo | .3125 | 8.10E-02 | 4 |
| | 1yr | .3820 | .2199 | 5 |
| | 3yr | .3333 | .1443 | 3 |
| | Total | .3467 | .1556 | 12 |

### Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| CUE | 2.4E-03 | 2 | 1.2E-03 | .088 | .916 | .175 | .061 |
| CUE * AGE | 1.3E-02 | 4 | 3.3E-03 | .238 | .913 | .952 | .090 |
| Error(CUE) | .247 | 18 | 1.4E-02 | | | | |

a. Computed using alpha = .05

### Tests of Within-Subjects Contrasts

Measure: MEASURE_1

| Source | Transformed Variable | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|---|
| CUE | CUE_1 | 5.3E-04 | 1 | 5.3E-04 | .056 | .818 | .056 | .055 |
| | CUE_2 | 1.9E-03 | 1 | 1.9E-03 | .104 | .754 | .104 | .060 |
| CUE * AGE | CUE_1 | 5.7E-03 | 2 | 2.9E-03 | .304 | .745 | .608 | .085 |
| | CUE_2 | 7.3E-03 | 2 | 3.7E-03 | .204 | .819 | .407 | .073 |
| Error(CUE) | CUE_1 | 8.5E-02 | 9 | 9.4E-03 | | | | |
| | CUE_2 | .162 | 9 | 1.8E-02 | | | | |

a. Computed using alpha = .05

### Multiple Comparisons

Bonferroni

| Dependent Variable | (I) age | (J) age | Mean Difference (I-J) | Std. Error | Sig. | 95% Confidence Interval | |
|---|---|---|---|---|---|---|---|
| | | | | | | Lower Bound | Upper Bound |
| LANDMARK | 5mo | 1yr | 1.000E-03 | .074 | 1.000 | -.2172 | .2192 |
| | | 3yr | 5.000E-03 | .085 | 1.000 | -.2434 | .2534 |
| | 1yr | 5mo | -1.00E-03 | .074 | 1.000 | -.2192 | .2172 |
| | | 3yr | 4.000E-03 | .081 | 1.000 | -.2335 | .2415 |
| | 3yr | 5mo | -5.00E-03 | .085 | 1.000 | -.2534 | .2434 |
| | | 1yr | -4.00E-03 | .081 | 1.000 | -.2415 | .2335 |
| LIGHT | 5mo | 1yr | -6.15E-02 | .122 | 1.000 | -.4206 | .2976 |
| | | 3yr | -8.75E-02 | .139 | 1.000 | -.4964 | .3214 |
| | 1yr | 5mo | 6.150E-02 | .122 | 1.000 | -.2976 | .4206 |
| | | 3yr | -2.60E-02 | .133 | 1.000 | -.4170 | .3650 |
| | 3yr | 5mo | 8.750E-02 | .139 | 1.000 | -.3214 | .4964 |
| | | 1yr | 2.600E-02 | .133 | 1.000 | -.3650 | .4170 |
| ODOR | 5mo | 1yr | -6.95E-02 | .113 | 1.000 | -.4006 | .2616 |
| | | 3yr | -2.08E-02 | .129 | 1.000 | -.3978 | .3561 |
| | 1yr | 5mo | 6.950E-02 | .113 | 1.000 | -.2616 | .4006 |
| | | 3yr | 4.867E-02 | .123 | 1.000 | -.3118 | .4091 |
| | 3yr | 5mo | 2.083E-02 | .129 | 1.000 | -.3561 | .3978 |
| | | 1yr | -4.87E-02 | .123 | 1.000 | -.4091 | .3118 |

### Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

| Source | Type III Sum of Squares | df | Mean Square | F | Sig. | Noncent. Parameter | Observed Power[a] |
|---|---|---|---|---|---|---|---|
| Intercept | 3.813 | 1 | 3.813 | 81.998 | .000 | 81.998 | 1.000 |
| AGE | 1.3E-02 | 2 | 6.6E-03 | .142 | .869 | .285 | .066 |
| Error | .418 | 9 | 4.6E-02 | | | | |

a. Computed using alpha = .05

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