SELECTIVE AND DIVIDED ATTENTION IN COMPARATIVE PSYCHOLOGY

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Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things to deal effectively with others.

—William James

Attention has been a central concept from the very beginnings of psychology. The quote from William James emphasizes how intuitive the notion of attention can appear. The passage also reflects James's functionalist roots by emphasizing the potentially adaptive value of attention, wherein lies its relevance to comparative psychology. An animal that can selectively attend to one of several possibilities could derive a significant advantage over another animal that cannot, and instead must devote comparable resources to all sensory inputs. Such selectivity is essential because not all environmental stimuli are equally important: The sound of an approaching predator, the colorful display of a conspecific, or the subtle odor of a scarce food may have critical consequences that demand an immediate response, and ought to take priority over the myriad of other, more trivial sensory inputs available at the same time.

Although attention is not a bit of terminology that has always been embraced by scientists studying animal behavior (e.g., behaviorism's rejection of mentalistic terms; see Sober, 1983), it nevertheless lies at the heart of many behaviors that have long been of interest to comparative psychologists and ethologists. Tinbergen's (1960) classic research on foraging, for example, reflects what many would now identify as selective attention. Tinbergen noted that seasonally abundant prey items made up a disproportionately large percentage of captures by great tits (*Parus major*), and proposed that foraging animals might use a "specific searching image" that enhances their ability to selectively identify high-frequency prey types. Although there has been some discussion over the nature of search images (Dawkins, 1971), the usefulness of such a selective process is not dependent on any specific underlying mechanism. An ability to efficiently identify high-probability targets would be potentially useful regardless of how those targets are identified. Nevertheless, the cognitive processes that give rise to such effective foraging tools are a valid and important target for research, and they have revealed insights into search images in a variety of species. For example, pigeons (*Columba livia*) are one of the most extensively studied animals in the cognitive and behavioral sciences, and laboratory experiments have shown that they also show search image effects when scanning for food targets, and that those search image effects can reasonably be interpreted as indicative of selective attention. Reid and Shettleworth (1992) presented pigeons with different types of grain on a gravel background. Grain types were visually discriminable from one another based on color, and different colored grains were presented in different proportions across sessions. If pigeons use a search image corresponding to the

more common grain type, they would be expected to overselect grains of that type. That is, they should select the more abundant grain at a rate even greater than would be expected based on its mere availability. When different grain types differed in distribution, pigeons did in fact select the more common type at a rate greater than could be expected if pigeons did not show a preference in their search process. Furthermore, experience with a specific grain type biased birds toward that same grain type on subsequent trials. Thus, their results show classic search image effects, and suggest that pigeons' attention could be primed to favor those features that best distinguished a frequent prey type from the background.

Langley, Riley, Bond, and Goel (1996) used a similar approach to investigate the circumstances under which search images are used. In particular, they proposed that search image effects might only be seen under circumstances when a search image would be beneficial (i.e., when prey items are difficult to discriminate from the background). They investigated this possibility by presenting different colorful seed types in two contexts. One context was a multicolored tray, in which seeds were difficult to see, mimicking the way cryptic prey take advantage of their natural camouflage in the wild. The other context was a grey tray, in which seeds visually stood out because their bright colors did not match the grey background. Although there was evidence that search images were activated whether seeds were cryptic or conspicuous, search performance was influenced by seed distributions only in the cryptic context (the colorful tray). When seeds were conspicuous, high and low density prey were easily visible and both were quickly consumed. When seeds were cryptic, the typical search image effect was seen, and high density types were overselected. In a separate experiment, they also found that a brief (3 min) delay was sufficient to deactivate a search image. This relatively quick change is important, in that it indicates that search images involve a dynamic cognitive process, rather than a slower, gradual process such as associative learning. Based on their results, the authors argue convincingly that the notion of a search image conceptually parallels the concept of selective attention as it is normally

used in cognitive psychology. In particular, they propose that prey encounters serve as attentional cues, influencing the likelihood of perceiving subsequent targets. In that sense, those prey encounters parallel the kinds of visual signals or base-rate manipulations that are frequently used to manipulate attention in cognitive psychology labs. Furthermore, search images and selective attention are both useful specifically when discrimination is difficult. Easy discriminations, such as the identification of conspicuous prey, do not require attentional focus. Cryptic prey, on the other hand, necessarily require a difficult perceptual discrimination between the target and a similar background. Selective attention is one of the tools that make accurate performance possible on such difficult discriminations.

Much of the value of comparative psychology is tied to the variety of species it considers, and evidence for use of search images has been found in a number of different animals, using similar types of methods. Building on the previous research on great tits and pigeons, researchers have observed comparable search image effects in a variety of other bird species with varying lifestyles: blackbirds (*Turdus merula*; Lawrence, 1985), blue jays (*Cyanocitta cristata*; Pietrewicz & Kamil, 1979), and kestrels (*Falco tinnunculus*; Viitala, Korplmäki, Palokangas, & Koivula, 1995) all overselect abundant prey types. The relevance of search images is not limited to birds, however. Mammals such as the sea otter (*Enhydra lutris*; Ostfeld, 1982) also show patterns of prey selection indicative of search images. Furthermore, the same patterns are seen in several varieties of invertebrates, including bumblebees (*Bombus fervidus*; Heinrich, 1975), butterflies (*Battus philenor*; Rausher, 1978), and spiders (*Evarcha culicivora*; Cross & Jackson, 2010). An exhaustive listing of all animals that might use a search image is beyond the scope of this chapter, but note that those that the foraging habits of each match the features indicated as important by laboratory investigations: They feed on multiple prey types that vary in spatial distribution, and those prey types are cryptic but can, with attention, be distinguished from each other and from the background. In contrast, ambush predators (or "sit and wait" predators) would not be expected to use a search image, and instead would adopt

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other strategies to maximize gains (Pianka, 1966). Cornell (1976), for example, pointed out that undirected searchers, such as web-spinning spiders and antlions show little selectivity and take prey in proportion to their prevalence in the environment.

Note that the term *search image* should not be interpreted as exclusively visual, since animals can use other sensory modalities to forage in the same manner. Evidence for olfactory search images has been seen in the feeding patterns of yellowfin tuna (*Thunnus albacares*; Atema, Holland, & Ikehara, 1980) and skunks (*Mephitis mephitis*; Nams, 1997), and in the search strategies of trained explosive-sniffing dogs (*Canis familiaris*; Gazit, Goldblatt, & Terkel, 2005). Similarly, rattlesnakes (*Crotalus viridis*) use a chemical search image to identify prey (Melcer & Chiszar, 1989). Note again, that the variety of search-image modalities (like the diversity of search-image utilizing species) does not imply that search images are universal. They should be used specifically by those species that must perform a difficult discrimination (visual or otherwise) during a directed search.

Given these parallels between search images and selective attention, as well as the fact that many other topics in comparative psychology (memory, perception, serial learning, etc.) have benefitted from theories grounded in cognitive psychology, an understanding of theories of human attention may prove to be a useful tool in the arsenal of the comparative psychologist interested in attention. Broadbent (1958), for example, characterized attention as a selective filter that could be used to limit incoming information to a more manageable amount, and this characterization of attention as a filter resonates with the previous research on search images, in that they seem to play a similar filtering role during foraging. In fact, much of what we now know about various aspects of attention in animals has been inspired by methods and theories developed over decades of research on human attention.

Consequently, this chapter aims to provide an overview of research on the various aspects of selective and divided attention as they have been used in the field of comparative psychology. The general approach will be to identify important elements of attention according to contemporary theories

of cognitive psychology, outline the methods that have been used to study those aspects of attention in humans, and then explore the ways in which those same concepts and methods have been used to study animal cognition. Given this approach, there will naturally be a bias toward visual attention (the primary sensory modality for humans, the original source of data from which the theories are derived), and animal species that are widely used in laboratory research. However, this does not imply that the concepts are not also applicable to other animals or sensory modalities, and such broader applicability will be acknowledged wherever possible.

SELECTION OF FEATURES

One of the most influential theories of human selective attention is Treisman's feature integration theory (Treisman & Gelade, 1980). The theory proposes that perception involves two stages: an early, preattentive stage, in which individual features of an object (e.g., color, shape, movement) are each automatically but separately processed; and a late, focused attention stage, in which individual features are combined into a more sophisticated, integrated perception of an object. A popular metaphor characterizes attention as the "glue" that binds together the various features of an object. Feature integration theory implies that some kinds of search tasks can be performed quickly and without attention (specifically, those relying on a single feature), whereas others require attention (those that rely on a conjunction of features), resulting in a slower, more effortful process.

Compelling evidence for feature integration theory comes from visual search tasks using stimuli that have been carefully designed to recruit either early or late stage processing. *Feature searches* involve only a single feature such as color, shape, orientation, or direction of movement, and according to feature integration theory can be done quickly and in a parallel fashion. *Conjunction searches* on the other hand, involve a combination of features (assumed to require attention), and must be done in a slower, serial fashion (Treisman, 1986). For example, an area consisting of grey shapes stands out within a field of white shapes because a search can be based on a single feature (color). Targets in

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feature searches are usually identified very quickly, regardless of the number of distractors. In contrast, conjunction searches (based on a combination of two features such as shape and color) typically produce much slower response times. For example, an area consisting of white squares and grey circles is not nearly as noticeable within a field consisting of grey circles and white squares (see Figure 9.1). Attention is required to bind together the combination of features that defines the target area. These results support one of the primary principles of feature integration theory: Not all visual searches are done in the same way.

Cook (1992) asked whether pigeons' visual searches also used distinct early and late stage processes depending on the type of search. Using
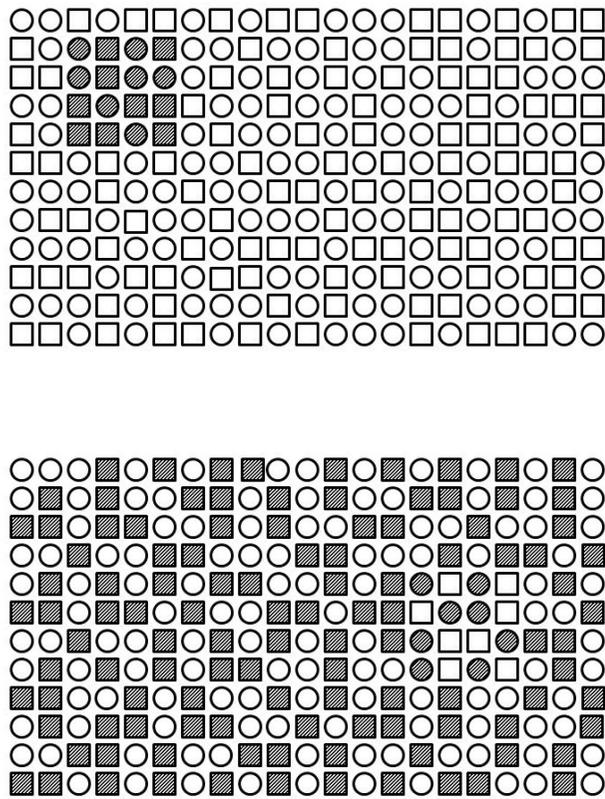

FIGURE 9.1. **Visual search stimuli used to study feature integration theory. Top: A small area defined by a single feature (dark squares and circles in the top left quadrant, surrounded by light squares and circles) usually stands out. Bottom: A small area defined by a conjunction of features (light squares and dark circles in the lower right quadrant, surrounded by dark squares and light circles) is more difficult to identify and requires attention.**

stimuli patterned after those developed by Treisman, he trained pigeons to peck the odd region of an otherwise uniform texture display. For example, in a feature search, pigeons might search for a small region of red squares embedded within a field of green squares. In a conjunction search, pigeons might search for a small region consisting of red squares and green circles embedded within a field of red circles and green squares. Pigeons' accuracy to peck the target region was lower on conjunction searches than it was on feature searches (though still better than chance on both), consistent with the standard predictions of feature integration theory. These results suggest a two-stage process similar to that used by humans. Pigeons can use a feature search if only a single feature is sufficient for target identification, and the result is faster identification and higher accuracy. When searching for a conjunction of features, accuracy is poorer. Thus, the general pattern of results parallels the pattern seen in humans, and is consistent with the two-stage model proposed by feature integration theory.

The relevance of feature integration theory is not limited to humans and pigeons. Bichot and Schall (1999) took a similar approach to investigating visual search in macaque monkeys (*Macaca mulatta* and *Macaca radiata*). Monkeys were trained to make an eye saccade toward a target in a visual display defined either by a feature of a conjunction of features. They performed better than chance on both kinds of searches, as humans and pigeons can. Furthermore, response times increased with set size for conjunction searches, but not for feature searches. This primary result is also consistent with Treisman's (1986) proposed two-stage model, where feature searches are done in parallel, whereas conjunction searches are serial.

The parallels between feature and conjunction searches on the one hand, and conspicuous and cryptic prey on the other, make a case for the ecological relevance of selective attention, and also provide some valuable insight into the mechanisms that may underlie the foraging behavior observed in natural settings by Tinbergen (1960). Animals, like humans, can search based on specific features or based on conjunctions of features, and depending on the type of search image, the process might

require attention (conjunction searches and cryptic prey) or might not (feature searches and conspicuous prey). However, this is not the only way attention can be used to selectively favor processing of certain kinds of stimuli.

SELECTION OF SPATIAL LOCATIONS

Attention can also be used to select specific spatial locations, and cognitive psychologists have likened it to a spotlight that can move around one's field of vision (Posner, 1980). Objects falling within the spotlight receive enhanced processing relative to those in other regions. Note that attention in this sense is different from direction of gaze (see Chapter 32, this volume). In many situations, one can make maximal use of an unequal distribution of visual receptors on the retina by directing one's fovea (with its maximal density of photoreceptors) toward important areas of the environment (see Chapter 3, this volume). Humans, for example, read by moving the fovea across a line of text. However, this is not the only way of enhancing the processing of a spatial location. *Covert attention* involves attending to a location without looking directly at it. A point guard in a basketball game might, for example, disguise his intentions by looking in one direction while passing the ball in a different one. His attention is engaged on a passing target, and that target's location does not correspond to his foveal fixation point.

To investigate this aspect of attention, Posner, Snyder, and Davidson (1980) had human participants monitor a display for the onset of a light that could occur either to the left or to the right of a fixation point. On some trials, a brief flashing cue to the left or to the right of fixation provided probabilistic information about the location of the upcoming target. In particular, the cue appeared in the same location as the following target 80% of the time (called *valid cues*). The remaining 20% of the time, the cue appeared in the opposite location (*invalid cues*). Figure 9.2 provides schematic depictions of trials featuring valid and invalid cues. Participants learned to anticipate targets on validly cued trials, in that their response times were faster to validly cued targets than they were to uncued targets that appeared without any preceding cue. This result was

consistent even though participants' eyes remained anchored to the central fixation point, indicating that the response time facilitation was due to a shift of attention and not to a peripheral cause, such as anticipatory eye saccades. Correspondingly, invalidly cued targets produced response times that were slower than those on uncued trials (and by extension, validly cued trials). Response times increased on invalid trials because attention had been directed away from the eventual target by the invalid cue, and that additional distance had to be covered before a response could occur. Again, these results indicate that attention can be directed to specific regions of space, and are consistent with the characterization of attention as a spotlight that can be preferentially directed to those locations that are likely to be important.

Shimp and Friedrich (1993) asked if pigeons would show similar control of spatial attention by developing a parallel task in which left and right targets were preceded by either valid (same spatial location) or invalid (different spatial location) predictive cues. Targets were red keylights appearing on one of the side keys in an operant chamber, and pecks to lit targets were reinforced with grain. Predictive cues were presented on each trial, consisting of brief (50 ms) white lights that preceded the target by various intervals of time. Their results followed the expected pattern: Response times to validly cued targets were faster than response times to invalidly
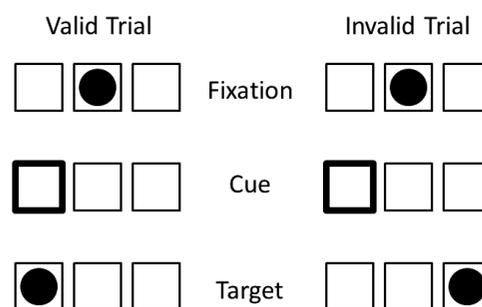

FIGURE 9.2. Schematic of valid and invalid trials in a spatial cueing task. Left: A valid trial, in which the spatial cue appears in the same location as the subsequent target. Right: An invalid trial, in which the spatial cue appears in a different location than the subsequent target. Response times to validly cued trials are consistently faster than response times to invalidly cued trials.

cued targets. This finding indicates that pigeons' attention can also be directed to different spatial locations, giving them preferential processing and producing response time facilitation. In addition, it indicates that attention shifts can occur over short time periods (i.e., the short duration between a cue and the subsequent target, using values as low as 150 ms). Note that in this operant task, direction of gaze could not be measured, as it is in the human research. Thus, on longer duration trials, pigeons could have adopted a strategy wherein they move toward the cued location and respond on the nearest available option, which would indicate a peripheral, rather than a central attentional mechanism. Such a strategy however, would be less effective on trials with short intervals, because they limit the necessary travel time. In addition, other lines of research point toward central attentional processes in similar tasks. Stonebraker and Rilling (1984) for example, used a matching to sample task, in which color samples were paired with either color comparison stimuli (identity matching) or line orientation comparison stimuli (symbolic matching). On each trial, a cue was presented along with the sample, indicating which type of comparison stimuli were to follow. Birds correctly matched both kinds of stimuli, but were impaired on occasional probe trials on which the comparison stimuli did not correspond to the type indicated by the cue. This result is indicative of prospective coding (rather than retrospective), but more important, since the location of the correct response was not cued, the cueing effect could not be accounted for by a peripheral orienting mechanism. Thus, it appears that pigeons, like humans, can direct their attention on a moment-to-moment basis if such rapid shifts are demanded by the situation.

A related phenomenon of spatial attention originating in the study of human cognition is the Simon effect. Simon (1968) noted that response times to visual stimuli were dependent on the required response. In particular, participants were faster to respond to a target if spatial aspects of the required response coincided with the location of the cueing stimulus. For example, if a participant is required to press a left response button when seeing any red light and a right response button when seeing any green light, response times are fastest if the light cue is presented on the same side

as the relevant response button. In this example, the required left button press is faster if cued by a red light appearing to the left (*corresponding trials*) than if cued by a red light appearing to the right (*noncorresponding trials*). Similarly, right button presses are faster to an ipsilaterally presented green cue than to a contralaterally presented green cue (Craft & Simon, 1970).

Urcuioli, Vu, and Proctor (2005) looked for a Simon-like effect in pigeons using the same logic. They presented pigeons with color stimuli on two response keys, and trained them to peck a specific key (left or right) when an associated color (red or green) was present on either key. For example, a red key (paired with an irrelevant white key in the other possible spatial location) meant that pecks on the left key would be reinforced, and a green key (again paired with an irrelevant white key) meant that pecks on the right key would be reinforced, regardless of whether the critical color itself appeared on the left or the right key. In this manner, corresponding trials were those on which the color signal corresponded to the response location (e.g., red–left/white–right or white–left/green–right). Noncorresponding trials were those on which the relevant red or green color stimulus did not coincide with the required response (e.g., white–left/red–right or green–left/white–right). Their results showed accuracy and response time advantages for corresponding trials over noncorresponding trials, similar to the standard Simon effect seen in humans.

The existence of a parallel Simon effect in pigeons indicates several things. Primarily, it is another example of flexible spatial attention: Attention can be directed to different spatial locations based on a number of different features, and those features need not be spatial, as they are in Posner's cueing method. Second, although pigeons (and people) have control over attention, it is still influenced by nonarbitrary factors. The Simon effect decreases response times specifically on corresponding trials, in which the response specifically matches the location of the cue.

Again, such spatial aspects of selective attention are not limited to humans and pigeons. Rats (*Rattus norvegicus*) show standard cueing effects in a Posner-like spatial cueing task (Marote & Xavier, 2011), as well as a Simon effect (Courtière, Hardouin, Burle, Vidal, & Hasbroucq, 2007), pointing to

similarly flexible control of spatial selective attention. In addition, Eckstein et al. (2013) adopted the spatial cueing method for humans, macaque monkeys, and honey bees, finding a spatial cueing effect in all three, though the strength of the effect was not uniform: Humans showed the strongest effect, and honey bees the weakest. Thus, although multiple species show spatial cueing effects, the details of how the "spotlight" operates may not always be identical across species.

SELECTION OF HIERARCHICAL LEVELS

Shifts of attention from one location to another are important, but reflect only one way that the spatial aspects of attention can be manipulated by an individual. Certain situations may instead (or also) require a shift of attention between hierarchical levels of visual organization. A common example of this kind of hierarchical organization would be the perception of a forest and its component trees. Individuals can choose to attend to a global level of analysis (the forest) or, if the situation demands, shift to a local level (a specific tree; see Chapters 5 and 8, this volume). Thus, rather than a spotlight, one might instead use a zoom lens as a metaphor for attention, reflecting the fact that attention can also be adjusted in size, encompassing a larger or smaller area. Navon (1977) investigated this kind of local/ global attention dynamic in humans using stimuli having hierarchical structure like those depicted in Figure 9.3. Note that each stimulus consists of a larger configuration made up of smaller individual characters. Identification of the larger configuration requires a wider, global scope of attention, large enough to encompass multiple local characters. In contrast, identification of one of the individual characters requires a narrower, local level of attention independent of their configuration or context. Navon found that human participants could shift attention to either the local or global level of analysis as necessary, but that all other things being equal, humans had a tendency to prioritize more highly the global level of analysis in that they identified global targets more quickly than local targets.

Several animals can also process local and global aspects of stimuli with hierarchical structure,

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    T     T               HHHHH
    T     T                   H
    TTTTT                     H
    T     T                   H
    T     T                   H

  Global H / Local T       Global T / Local H
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FIGURE 9.3.   Hierarchical stimuli used to investigate local/global attention. Stimuli consist of a collection of local letters, arranged into a global configuration. A given letter (T or H in these examples) can appear either at the local or global level.

including fish (*Xenotoca eiseni*; Truppa, Sovrano, Spinozzi, & Bisazza, 2010), domestic chicks (*Gallus gallus*; Chiandetti, Pecchia, Patt, & Vallortigara, 2014), pigeons (Fremouw, Herbranson, & Shimp, 1998, 2002), domestic dogs (Pitteri, Mongillo, Carnier, & Marinelli, 2014), capuchin monkeys (*Cebus paella*; Spinozzi, De Lillo, & Salvi, 2006), rhesus macaques (Hopkins & Washburn, 2002), baboons (*Papio papio*; Deruelle & Fagot, 1998), and chimpanzees (*Pan troglodytes*; Fagot & Tomonaga, 1999; see also Chapter 5, this volume).

Fremouw et al. (1998), for example, asked if pigeons could identify local and global features of a stimulus display, and if so whether they could shift attention between local and global levels of analysis. Pigeons were presented with hierarchical stimuli like those in Figure 9.4, and trained to search for specific letter targets that could occur at either the local level or the global level. For example, presence of the letter H meant that a left response would be reinforced (whether it appeared at the local or the global level), whereas the letter S meant that pecks to the right key would be reinforced (again regardless of its hierarchical level). Pigeons learned to respond accurately to targets presented at either level. Furthermore, by presenting successive blocks of trials, during which the preponderance of targets appeared at one level or the other, they showed that birds could be primed to preferentially search at a specific level. When 85% of targets appeared at the local level, and 15% of targets appeared at the global level, response times were faster to targets appearing at the local level. Conversely, when 85% of targets appeared at the global level, the response time advantage was reversed, and pigeons were faster to

Element Samples

Compound Samples
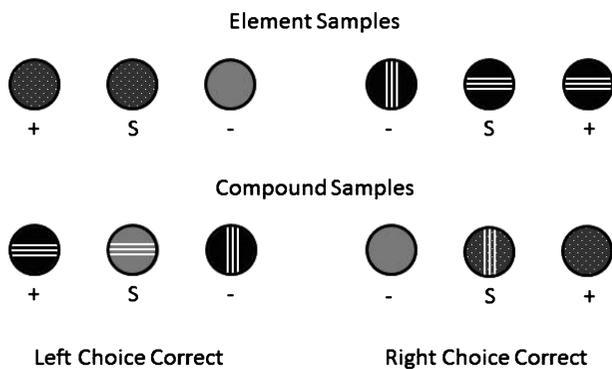

Left Choice Correct   Right Choice Correct

FIGURE 9.4.   Matching-to-sample task used to investigate divided attention. Top: Element sample trials, in which the sample (center key) consists of either a color or line orientation. Comparison stimuli (side keys) are of the same type (color or line orientation) as the sample. The correct comparison stimulus is the one that matches the sample. Bottom: Compound sample trials, in which the sample consists of both a color and line orientation. Comparison stimuli (side keys) consist of a single element (either colors or line orientations). The correct comparison stimulus is the one that matches an element from the sample.

respond to targets at the global level. Thus, birds showed an ability to flexibly shift the hierarchical aspect of attention to take advantage of the base rates at which local and global targets appeared.

In a subsequent experiment, Fremouw et al. (2002) looked into the requisite time frame for these kinds of local/global attention shifts. The blocking procedure mentioned previously involved shifts of attention over the course of many trials across several days. This left open the question of whether pigeons could shift attention between local and global levels on a moment-to-moment basis. To answer this question, they used a trial-by-trial cueing procedure, in which a brief visual cue predicted (with 85% accuracy) the level at which an upcoming target was to appear (but not the specific target or the required response). This cueing procedure produced an effect that paralleled the earlier blocking procedure: Response times were faster to targets at the primed level than to targets at the unprimed level. This pattern of results indicates that pigeons can indeed flexibly shift their level of attentional focus based on a number of factors, and if necessary can do so quickly.

Recall that although humans can flexibly shift attention between local and global levels of analysis,

Navon (1977) also found that they showed a global precedence in that they identified targets at the global level more quickly than targets at the local level. Cavoto and Cook (2001) investigated whether pigeons might also show a precedence effect, and if so, whether it would mirror humans' global precedence. Like Fremouw et al. (1998, 2002), they presented hierarchical stimuli having a target at either the local or global level, and compared accuracy on local and global targets during learning. Their results pointed toward a local precedence (notably opposite that of humans), in that birds learned to accurately identify local targets earlier in training than they did global targets. In a subsequent experiment, they presented pigeons with stimuli featuring conflicting local and global information (i.e., targets at both levels, each associated with different responses). On these conflicting probe trials, pigeons were more likely to respond in a manner consistent with the target presented at the local level.

Note that this local precedence in pigeons is different from the human global precedence, but is consistent with the local precedence found in monkeys (Hopkins & Washburn, 2002; Spinozzi et al., 2006) and baboons (Deruelle & Fagot, 1998). Chimpanzees on the other hand, do not always process the local elements faster than global (Fagot & Tomonaga, 1999). Thus, although similar methods used to study local/global attention in primates, pigeons and humans, and although each species shows an ability to shift attention between levels, the details of how those attentional shifts happen are not always identical. Note that these differences could be due to attentional processes or to various procedural and anatomical constraints. Pigeons, for example, have a much broader visual field than primates due to their side-facing eyes, and are normally much closer to presented stimuli, to facilitate pecking responses.

DIVIDED ATTENTION

Although selectivity is a fundamental attribute of attention, attention can also be divided among multiple targets. However, there is often a cost to doing so: Divided attention is usually associated with a decrement in performance relative to situations that require attention to only a single element. A classic

example is the cocktail party effect (Cherry, 1953). In a situation where multiple channels of information are available, one can selectively attend to one channel, as when one focuses on a single conversation partner at a crowded and noisy cocktail party. One is bombarded by several voices, and all but one are effectively filtered out. Cherry (1953) studied the cocktail party effect using dichotic listening tasks, in which participants simultaneously listen to two different speech streams. Selective attention generally allows one to focus on one of the two speech streams, while filtering out the other. Attending to both is virtually impossible, and very little is extracted from the unattended speech stream. Although some information may break through from the unattended speech stream, this is limited to special cases, such as the participant's name, and is usually quickly forgotten (Moray, 1959). The same kinds of constraints seem to apply to visual attention as well. Neisser and Becklen (1975) used similar logic in a visual task, in which two videos were superimposed over one another, obtaining parallel results: When asked to monitor one video and ignore the other, participants were quite successful, and could report accurately on the contents of the attended (but not the unattended) video. However, tracking both videos simultaneously proved virtually impossible. Thus, the limitations of attention, and the costs of dividing it would seem to apply whether attending to auditory or visual stimuli.

The research programs described in previous sections show that pigeons are quite good at selecting specific aspects of a visual display (features, locations, or hierarchical levels). Given that pigeons' eye positioning provides them with a tremendous panoramic view of their environment, one might expect that there would be plentiful opportunities to select multiple simultaneous targets (i.e., divided attention). Maki and Leith (1973) investigated whether pigeons could simultaneously attend to two elements of a stimulus display, using a matching to sample procedure. Samples were presented on the center key in an operant chamber, followed immediately by comparison stimuli on both side keys, and pecks to the comparison stimulus that matched the sample were reinforced. On single-element trials, all stimuli were exemplars of the same type (either

colors or line orientations, but never a mixture of the two). On compound trials, samples consisted of a combination of two elements (a color and a line orientation presented on the sample key). Comparison stimuli on compound trials were the same as on single-element trials (consisting of a color or a line orientation, but never both), and the correct comparison stimulus was the one that matched either of the elements present in the compound sample. Thus, accurate performance on compound trials required that pigeons attend to both elements of the sample. Single-element trials did not require divided attention because the sample consisted of only one of the two possible elements. If there is a cost to dividing attention, then performance on single-element trials ought to be better than performance on compound trials. Indeed, Maki and Leith confirmed this expectation: Matching to sample accuracy was better when single-element samples were presented than when compound samples were presented. Note that there have been several alternative explanations proposed for this "element superiority effect" (see Zentall, 2012, for a comprehensive review). Nevertheless, superior performance on single-element trials comprises yet another similarity between established human results (the decrement in performance on divided attention tasks) and pigeons' performance on a parallel behavioral task (the element superiority effect). In both cases, there is a cost associated with simultaneous attention to multiple elements.

Similar divided attention effects have been shown in other animals. Dukas and Kamil (2001) presented blue jays (*Cyanocitta cristata*) with cryptic artificial prey on a computer monitor. Detection rates were lower when jays divided attention between searching for two different prey types at the same time, than when they searched for only a single prey type. Turchi and Sarter (1997) similarly studied divided attention in rats by requiring animals to perform a discrimination task requiring attention to either one or two possible modalities (visual or auditory). Not only was there a cost for attending to both modalities, but they were able to impair divided attention performance through a physiological manipulation. Although the neurological foundations of attention are beyond the scope of this chapter, they have been outlined elsewhere (see Posner, 2011), and this

finding underscores the fact that neuroscience can contribute to comparative psychology by providing useful frameworks and relevant data, much like the frameworks and data from cognitive psychology highlighted in this chapter (see Kesner & Olton, 1990).

SELECTIVE AND DIVIDED ATTENTION IN LEARNING AND CATEGORIZATION

As with many other cognitive processes (perception, memory, etc.), selective and divided attention can be thought of as general abilities that are available to be recruited for a variety of different purposes. For example, whereas learning is a fundamental behavioral process in its own right, it can also be influenced by attention (Nissen & Bullemer, 1987). In fact, classic research on discrimination learning was influenced heavily by ideas about selective attention. Lashley (1929) made an early acknowledgement that animals faced with a discrimination problem might not attend equally to all incoming stimuli. Based on that possibility, Krechevsky (1932) proposed that the characteristic learning curve in a sensory discrimination experiment is the result of an animal adopting a series of hypotheses, sequentially abandoning inadequate ones until reaching the successful solution. The adoption of a new hypothesis involves selective attention to a new aspect of the stimulus environment (e.g., a rat attending to brightness, after shape has proven to be an inadequate solution). This is an example of a noncontinuity theory, in that it assumes that an animal does not attend to all aspects of the environment during learning, but isolates one or more stimulus dimensions relevant to the current hypothesis. In favor of this position is the observation that discrimination learning is often abrupt, transitioning quickly from chance to virtually perfect performance, as well as the regular adoption of position biases during early training (assumed to correspond to incorrect hypotheses). In contrast, continuity theory (Spence, 1940) proposes that learning is a gradual process, with the cumulative response strength of all of the various stimulus components combining to determine a response at any one time. Although with proper assumptions, either kind of theory can indeed account for most of the discrimination

learning data, the important implication is that the concept of attention has important ramifications for learning (Mackintosh, 1965). That is, selective and divided attention have the potential to reach into—and influence other aspects of—cognition, such as learning and memory.

Another prominent and well-studied example of a cognitive process reliant on attention is categorization (see Chapter 5, this volume). Many animals, including humans and pigeons, learn to form useful categories that allow them to respond to novel stimuli in ways that are informed by past experiences (Goldstone & Kersten, 2003; Medin & Smith, 1984). Given that exemplars from natural categories vary along multiple dimensions (some of which are relevant to category membership and some of which are not), selective and divided attention would likely be essential components of category learning. Selective attention would allow an individual to focus on the relevant stimulus dimension (or dimensions) while ignoring the irrelevant ones. At the same time, divided attention would allow an individual to consider multiple relevant dimensions when they are jointly diagnostic of category membership.

Not surprisingly, numerous species can learn such multidimensional categories, including but not limited to chickens (Ryan, 1982), blue jays (*Cyanocitta cristata*; Pietrewicz & Kamil, 1977), African grey parrots (*Psittacus erithacus*; Pepperberg, 1983), squirrels (*Sciurus carolinensis*; Wills et al., 2009), domestic dogs (Range, Aust, Steurer, & Huber, 2008), horses (*Equus caballus*; Hanggi, 1999), squirrel monkeys (*Saimiri sciureus*; Roberts & Mazmanian, 1988), capuchin monkeys (D'Amato & van Sant, 1988), stumptailed monkeys (*Macaca arctoides*; Schrier, Angarella, & Povar, 1984), gorillas (*Gorilla gorilla*; Vonk & MacDonald, 2002), orangutans (*Pongo abelii*; Vonk & MacDonald, 2004), and chimpanzees (Hayes & Hayes, 1953). Given massive variation in methodology and categories, the specific cognitive processes used by each remain unclear.

Ashby and Gott (1988), however, developed a method that is well-suited to address such questions about multidimensional category learning, and that is simple and flexible enough to be used in comparative psychology. They simulated categories using bivariate normal distributions, which mimic some of

the critical features of naturally occurring categories, while retaining experimental control of category structure and allowing for the relative importance of each dimension to be systematically and precisely manipulated. Figure 9.5 is a schematic of their method, and some conditions that can be derived to investigate attention to different attributes. The top left panel depicts two bivariate normal distributions (categories), from which stimuli can be drawn. The x- and y-axes represent two continuously varying dimensions on which stimuli can vary, such as height and width of rectangles, or frequency and orientation of Gabor patches (Yao, Krolak, & Steele,

1995). The z-axis represents the probability that a particular stimulus having attributes on the x- and y-axes will be drawn. Note that the center of a category consists of a dense collection of high-probability exemplars. As one moves away from the category center, exemplars become rarer in frequency and display less typical features (much like members of natural categories).

Categorization accuracy using this method is maximized by using a decision rule that best separates exemplars from the two category distributions. The optimal decision rule generally corresponds to a boundary, or line dividing the x–y plane such that
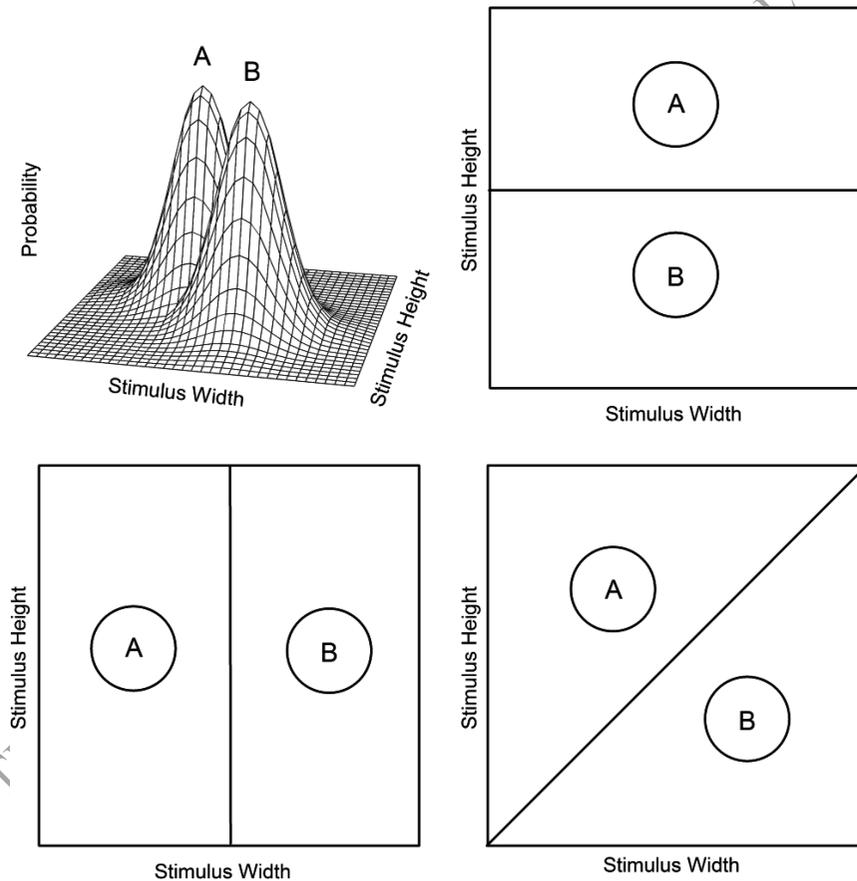

FIGURE 9.5.   Multidimensional categorization task. Top left: Two approximately normal distributions (A and B) from which stimuli can be sampled. Stimuli vary along two dimensions (e.g., height and width). Top right: Summary of a categorization task requiring selective attention to height. Letters indicate peaks of each category distribution. Solid circles correspond to stimuli equally likely to be drawn from a given category. Dashed line indicates points where the two categories intersect, resulting in stimuli equally likely to be drawn from either category and corresponding to the optimal decision boundary. Bottom left: Summary of a categorization task requiring selective attention to width. Bottom right: Summary of a categorization task requiring divided attention to both height and width.

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stimuli falling on opposite sides of the boundary will be categorized differently. If the centers of the category distributions differ on only one dimension, the boundary will be perpendicular to that axis (and parallel to the other), and accurate performance will require attention to only a single dimension (top-right and bottom-left panels in Figure 9.5). On the other hand, if the centers of the distributions differ on both dimensions, the optimal boundary will be oblique, and accurate performance will require attention to both dimensions (bottom-right panel in Figure 9.5). When presented with stimuli generated from categories that differ on only one dimension, human participants selectively attend to the relevant dimension, using a decision bound perpendicular to the diagnostic axis. When presented with stimuli from categories that can only be discriminated by dividing attention among both dimensions, human participants are capable of incorporating both dimensions into their categorization decisions, and use a decision bound that reflects the influence of both dimensions.

Herbranson, Fremouw and Shimp (1999, 2002) used the same method to investigate categorization in pigeons using either rectangles differing in height and width or moving dots varying in speed and direction. When categories differed on a single dimension, pigeons' responses were controlled by the relevant dimension, and uninfluenced by the randomly varying irrelevant dimension. Pigeons also responded accurately when categories could only be differentiated by attending to both dimensions, indicating that they were able to incorporate information from both dimensions. Thus, pigeons were able to selectively attend to one dimension, or divide attention among two dimensions as required by the categories in effect (see Chase & Heinemann, 1972, for a similar approach).

Smith et al. (2012) used this method to investigate categorization in pigeons and three primate species: humans (*Homo sapiens*), rhesus macaque, and capuchin monkeys. Accurate performance on some conditions required attention to only one of two varying stimulus dimensions (the second varied randomly and was not diagnostic of category membership). Other conditions required attention to both dimensions, in that accurate performance

was not possible without considering both stimulus dimensions. They found that pigeons could learn both kinds of categories, and that they learned both at approximately the same rate. Thus, pigeons could selectively attend to a single stimulus dimension (filtering out the other, randomly varying dimension) or divide attention among both. Meanwhile, all three primate species also learned both kinds of categories, but learned single-dimension categories more quickly than information integration categories. Thus, even though all species learned both kinds of categories, interspecies differences suggested that the cognitive tools used to do so may not have been the same for each.

LIMITATIONS AND FAILURES OF ATTENTION

Attention has been traditionally characterized as a limited resource, or information processing bottleneck. Although these characterizations originate in the study of human cognition, note that the relevant pattern of results has been generally replicated in animals: Tasks that demand more from attention result in poorer performance. Recall for example, that accuracy is impaired in visual search tasks that are defined by a conjunction of features relative to searches based on a single feature (Cook, 1992) and that matching to sample tasks with a compound sample are more difficult than tasks with a single-element sample (Maki & Leith, 1973).

Another notable demonstration of attention's limits is the phenomenon of change blindness, in which normally conspicuous changes to a stimulus display often fail to capture attention under certain specific conditions. Rensink, O'Regan, and Clark (1997) used a simple change detection task to study the conditions under which human participants would fail to notice a change. Two images, identical save for a single localized difference, were presented in successive alternation. When transitions between subsequent images were instantaneous, the changes "popped out" and were spotted almost immediately by participants. In contrast, when there was a brief interstimulus interval (ISI) between images, the change was more difficult to detect: Participants required more time to spot the difference,

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and performed at lower levels of accuracy. Rensink et al. also found that in the more difficult condition (featuring the ISI), changes of central interest (pertaining to the primary subject matter of the image) were spotted more quickly than changes of marginal interest. This feature of change blindness presumably serves to minimize the potential negative consequences the attention bottleneck: Changes of central interest are more likely to carry important consequences, and are thus favored for selection early in the search process.

Attention may play a similar selection function in animals, and if so, we might see comparable limitations in change detection. Laboratory investigations show that pigeons and rhesus monkeys are indeed capable of monitoring a display for change, and their performance is similar in many ways to that of humans (Cook, Katz, & Blaisdell, 2012; Elmore, Magnotti, Katz, & Wright, 2012; Leising et al., 2013). Herbranson et al. (2014) built on this change detection research by developing an analog of Rensink

et al.'s (1997) flicker task that could be presented to pigeons in an operant chamber (Figure 9.6). Pigeons were presented with alternating stimulus displays consisting of line orientation elements spread across three response keys. An original and a modified display consisted of the same line features, with one exception. A single line feature was added to or deleted from the original display to create a similar, but nonidentical modified display. Individual trials featured pairs of displays, alternated for varying numbers of repetitions, and either with or without an ISI. In parallel with human change blindness results, accuracy was consistently lower on trials featuring an ISI (but still greater than chance). Furthermore, pigeons' accuracy increased with added repetitions, and patterns of responding indicated that birds had used a serial search strategy, progressing from one location to another until the change was identified. As with humans, it appears that timing has a powerful influence over selection: The presence of an ISI between subsequent
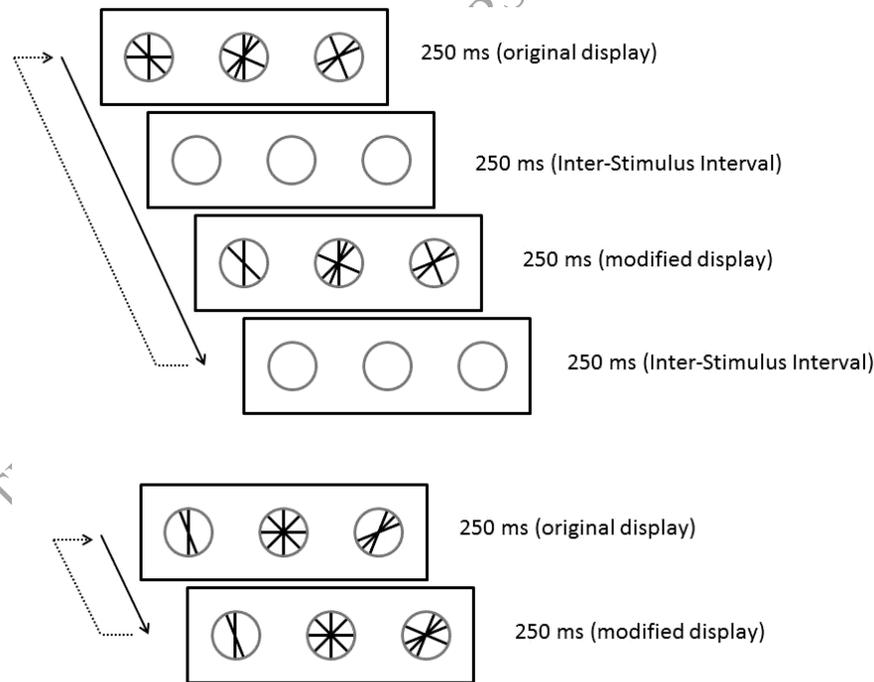

FIGURE 9.6.   Example of a change detection trial using the flicker paradigm, in which two non-identical stimulus displays are alternated. Top: A trial with an inter-stimulus interval (ISI), in which there is a blank interval between each consecutive stimulus display. The correct response is to peck the key that is not the same (left key). Bottom: A trial with no ISI, in which consecutive stimulus displays are contiguous, with no intervening time delay. The correct response is to peck the key that is not the same (right key).

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displays makes change detection more difficult. Change blindness indicates that not all incoming information can be processed, and that pigeons (like humans) must select partial information from the available channels.

Change detection would seem to be a critical cognitive ability, essential to a variety of activities (Rensink, 2002), and this feature makes change blindness all the more fascinating as a limitation of visual attention. Nevertheless, such a limitation is consistent with the constraints placed on other aspects of attention (the decrements in performance associated with conjunction searches, invalid cueing, and divided attention, for example). Given that animals can learn to use search images, cue information, and category structures to direct attention in strategic ways, one might also predict that animals could devise strategies to counter the negative consequences of change blindness. Cavanaugh and Wurtz (2002) found evidence for this possibility, testing rhesus macaques for change blindness, using a procedure similar to Herbranson et al. (2014). Although they still found a standard change blindness effect, change detection was improved (in terms of accuracy and response time) on trials when the location of an upcoming change was cued in advance. That is, monkeys could use predictive cues to direct their search in ways that reduced (but did not eliminate) change blindness.

CONCLUSION

The research summarized here indicates that many animals are capable of directing attention in many of the same ways humans do: They can select specific features, spatial locations, or hierarchical levels for preferential analysis, as the situation might demand. Furthermore, animals can divide attention and consider multiple aspects of their environment simultaneously, though such division may be accompanied by a decrement in performance. These fundamental processes of selective and divided attention are used in many cognitive processes including but not limited to discrimination, categorization, and change detection. Finally, as useful as attention is, it is not flawless, and is subject to strict limitations that can lead to systematic failures of selection such as change blindness.

Most of the general features of selective and divided attention in animals approximately parallel those same features of selective and divided attention in humans. Nevertheless, although the same general principles apply to multiple species, some of the details differ, and those differences are presumably due to the different environmental demands faced by the species in question. Pigeons and several species of primates, for example, seem to have a bias toward attending to the local aspects of hierarchical organization whereas humans display a global precedence (Cavoto & Cook, 2001). In addition, differential learning rates indicate that pigeons do not learn categories requiring selective and divided attention the same way that humans and other primates do (Smith et al., 2012). The contrast in how these common attentional abilities are implemented in different species are useful, in that they may provide some insights into the evolutionary origins of attention and other cognitive abilities. Smith et al. (2012), for instance, proposed that the category learning differences between pigeons and primates may reflect an important step in the evolution of explicit cognition.

The research reviewed in this chapter suggests that many of the fundamental elements of attention according to contemporary theories of human cognition can be applied in similar fashion to animals. However, one should be careful to not assume that they are universally applicable. In particular, note that most of these theories derive from research specifically on visual cognition in humans. This visual bias in research and theory is perhaps not surprising, given that visual input tends to dominate other modalities in humans (Posner, Nissen, & Klein, 1976). In turn, much of the comparative research motivated by those theories has used variations on the same visual tasks, using animals like pigeons that also show a visual dominance (Randich, Klein, & Lolordo, 1978). Nonvisual tasks or species that do not show such a strong visual bias might or might not produce the same strong parallel. Given that some of the most compelling research on selective and divided attention in humans comes from dichotic listening tasks (e.g., Cherry, 1953), the theoretical importance of auditory attention in animals should not be ignored. In fact, a wide variety of animals are indeed capable of selectively

attending to individual features of complex sounds such as quality or location, while ignoring others (Heffner, 1998). Thus, there is evidence that the useful aspects of selective and divided attention can extend to other (nonvisual) sensory modalities in humans and animals. As always, much of the value of comparative psychology will rely on its ability to consider a diverse array of animals and tasks.

Finally, these programs of research have demonstrated that many of the models and theories used to study human attention can be similarly useful in the study of selective and divided attention in animals. Zentall (2013) argued that theories imported from human cognitive psychology might or might not lead to comparable results in nonhuman animals, but they do frequently motivate undeniably useful and informative experiments that would not otherwise have been conducted. In the context of the present topic for example, it is unlikely that research on local/global attention (Fremouw, Herbranson, & Shimp, 1998), the Simon effect (Urcuioli et al., 2005), or feature integration theory (Cook, 1992) would have happened in the same way without the preceding theories of human attention by which they were motivated (Navon, 1977; Simon, 1968; Treisman & Gelade, 1980). Associative learning mechanisms of course, remain an essential foundation for the study of animal behavior, but can and should be tested against predictions made by cognitive theories, such as those developed during the long history of research on selective and divided attention (e.g., Broadbent, 1958). Again, in the context of the research provided here, associative learning by itself might account for some search image effects occurring over slower time scales (Tinbergen, 1960), but the rapid shifts demonstrated in laboratory experiments (Langley et al., 1996) emphasize the usefulness of including attention in an understanding of the phenomenon.

Use of cognitive theories is furthermore appealing from a modern interdisciplinary perspective, in that it embraces potential contributions from other areas of cognitive science. For example, learning theories can benefit from an understanding of biological principles such as natural selection and genetics, which constrain and shape fundamental learning mechanisms (Papini, 2002). It is likely that the study of animal behavior could similarly benefit

from concepts from other related fields such as computer science or behavioral economics. Future research will hopefully continue to add to our knowledge about attentional processes in pigeons, and further refine theories that give those data biological and psychological meaning.

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