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Visual Search and Decision Making in Bees: Time, Speed, and Accuracy

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An insect searching a meadow for flowers may detect several flowers from different species per second, so the task of choosing the right flowers rapidly is not trivial. Here we apply concepts from the field of visual search in human experimental psychology to the task a bee faces in searching a meadow for familiar flowers, and avoiding “distraction” by unknown or unrewarding flowers. Our approach highlights the importance of visual information processing for understanding the behavioral ecology of foraging. Intensity of illuminating light, target contrast with background (both chromatic and achromatic), and number of distractors are all shown to have a direct influence on decision times in behavioral choice experiments. To a considerable extent, the observed search behavior can be explained by the temporal and spatial properties of neuronal circuits underlying visual object detection. Our results also emphasize the importance of the time dimension in decision making. During visual search in humans, improved accuracy in solving discrimination tasks comes at a cost in response time, but the vast majority of studies on decision making in animals have focused on choice accuracy, not speed. We show that in behavioral choice experiments in bees, there is a tight link between the two. We demonstrate both between-individual and within-individual speed-accuracy tradeoffs, whereby bees exhibit considerable behavioral flexibility in solving visual search tasks. Motivation is an important factor in selection of behavioral strategies for a search task, and sensory discrimination capabilities may be underestimated by studies that quantify accuracy of behavioral choice but neglect the temporal dimension.

To someone studying social insects, vertebrate behavior is sometimes surprisingly dull. Among the social insects, such as termites, ants, bees and wasps, we find agriculture, slavery, territorial wars, castes, division of labor, consensus building, a symbolic language, and teeming cities with fantastic architecture (Frisch, 1967; Hölldobler & Wilson, 1990; Seeley, 1995). The cognitive capacities of social insects are likewise impressive. Bees, in particular, have recently revealed a number of abilities traditionally only attributed to a few higher vertebrates (e.g. pigeons, dolphins, primates), such as sequence learning, object categorization, concept formation, and a simple form of counting (Chittka & Geiger, 1995; Collett, Fry, & Wehner, 1993; Giurfa, 2003; Menzel, 2001; Srinivasan, Zhang, & Rolfe, 1993). All of this, of course, was in place millions of years before humans graced the planet. This is all the more remarkable given that a bee’s nervous system contains less than a million neurons (Giurfa, 2003), or only 0.001% of the number of neurons that the human brain possesses.

Occasionally, however, research on another interesting animal, *Homo sapiens*, has produced concepts that are useful in their application to social insects. The psychology of visual search is one such case (Desimone, 1998). Interestingly, the typical tests run by psychologists seem more appropriate to a bee's world than to a human's. Commonly, subjects are asked to search a display for one or several defined targets (such as a small yellow square). The targets may either move across the screen from the periphery, or may appear at certain locations in the center of the screen, and they are commonly mixed with other stimuli (distractors), which differ from those the subject is asked to search for (Downing & Pinker, 1985; Zenger & Fahle, 1997). Targets may differ from distractors in one stimulus dimension only (such as color), or they may differ in several dimensions (such as color and shape). Performance of subjects is evaluated in terms of reaction time and accuracy, and in terms of the individual strategy used to optimize the speed-accuracy tradeoff (Treisman & Gormican, 1988; Wolfe, 1999).

Note the similarity with an insect searching a meadow for familiar rewarding floral signals. Bees need to identify flower species with high pollen and nectar rewards and short handling times, and use sensory cues (flower scents and colors, patterns, size, plane of symmetry etc.) to memorize these flowers (Benard, Stach, & Giurfa, 2006; Chittka, Thomson, & Waser, 1999; Gould, 1985). The market can be complex – bees will typically have to choose between several dozen flower species which all differ in reward and signal, and they may encounter several flowers with different signals per second of flight (Chittka et al., 1999). To maximize fitness, bees need to harvest as much pollen and nectar in as little time as possible. Avoiding errors (e.g. visits to non-rewarding flowers) is only critical if the investments into increased accuracy are offset by overall gains in rewards harvested per unit time. Here we review the sensory and cognitive factors that affect decision speed in foraging bees, and their interplay with accuracy. Our particular emphasis is on speed, however, since most studies in the field, to date, have focused on the accuracy with which bees perform foraging tasks (Chittka, Dyer, Bock, & Dornhaus, 2003). In the natural lives of bees, however, speed of choice may often be of more important than accuracy. We draw on concepts from one of the most dynamic fields of experimental psychology, visual search.

Target Size, Illumination, and Visual Constraints on Search Time

Before we can explore how search strategies may reflect underlying cognitive factors in decision making, we need to consider the visual world of a bee. Detecting a familiar target, such as a flower of particular size, color and shape depends on the bee's visual system. How conspicuous is that flower to the bee? How do distance and illumination conditions affect detectability? In fact, flowers scattered in a green meadow present a bee with a considerable signal-to-noise problem (Chittka, Shmida, Troje, & Menzel, 1994).

The resolution of the compound eyes of bees is about 100 times worse than ours. Bee eyes are composed of several thousand functional units, the ommatidia, each of which contains its own lens and set of photoreceptors (Jander & Jander, 2002). In honeybees, for example, the resolving power of the ommatidial array is approximately 1° (Land, 1999). However, from the perspective of object detection and recognition, the spatial resolution of bee vision is not only limited by

the interommatidial angle, but also by subsequent processing. This is because the visual angle subtended by an object would presumably be required to cover more than a single ommatidium for object recognition. For example, for a target such as a 1 cm flower, to subtend a visual angle of 5° , a honeybee would have to view it from a distance of 11.5 cm (Giurfa & Lehrer, 2001). This implies that from the point of view of a bee in flight that was searching a meadow, target flowers would simply not be recognizable panoramically from a distance, and any search strategy used would necessitate relatively close approaches to potential targets. In accordance with this, search time for artificial flowers in a flight arena increases dramatically as flower diameter is decreased from 28 to 5 mm (Figure 1) (Spaethe, Tautz, & Chittka, 2001).

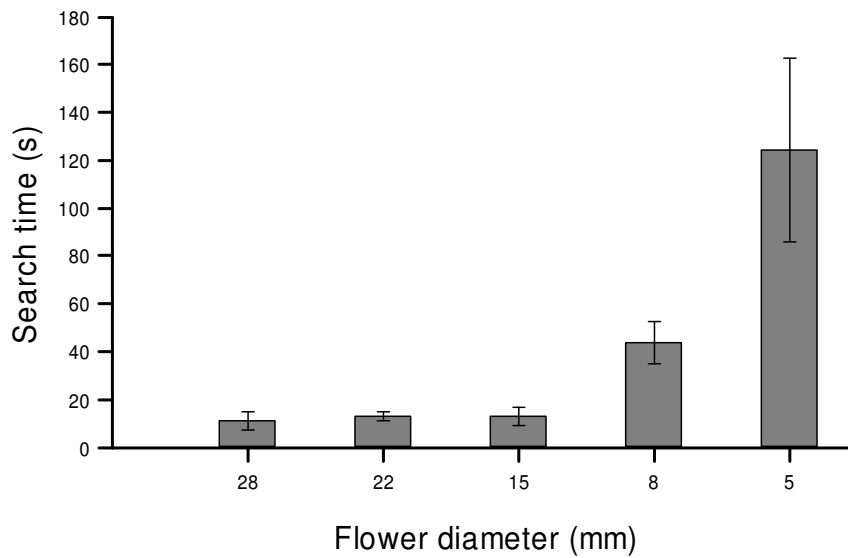


Figure 1. Floral search times of bumblebees increase as flower diameter decreases. One bumblebee at a time was allowed to enter a flight arena and search for the artificial white flowers. For each stimulus size three flowers of equal size were arranged in an equilateral triangle with a side length of 30 cm at random position in a flight arena. Search time (\pm SE; $N = 7$) was measured between bees' departure from the first flower until landing on the second one. For color properties of the flower and contrast to the background, see Spaethe et al. (2001).

For any receptor-based visual system, the signal-to-noise ratio improves with increasing light intensity (Kelber, Balkenius, & Warrant, 2002; Laughlin, 1981, 1989; Theobald, Greiner, Wcislo, & Warrant, 2006). Since bees forage under illumination conditions that can vary by several orders of magnitude, we asked whether this is a significant factor in determining search times for flowers of various sizes, and over a realistic range of intensities. We trained bumblebees (*Bombus terrestris*) to forage from circular artificial flowers of three sizes in a flight arena in a controlled illumination laboratory, (Figure 2; for methods see Spaethe et al., 2001). The intensity was controlled by placing ARRI gel filters over the arena (Dyer & Chittka, 2004a; we tested the bees' efficiency in finding flowers at 1,400, 700, 175 and 88 lux. For comparison, direct sunlight can be over 100,000 lux, 1,000 lux is the natural light intensity on a dull day, 500 lux is a recommended of-

fice lighting intensity, whereas intensities of around 100 lux might be expected after sunset or in understory vegetation, or under thick cloud cover (Williamson & Cummins, 1983; Kemp, 2002). Thus, we cover the intensity range at the lower end of intensity levels under which bumblebees might typically forage.

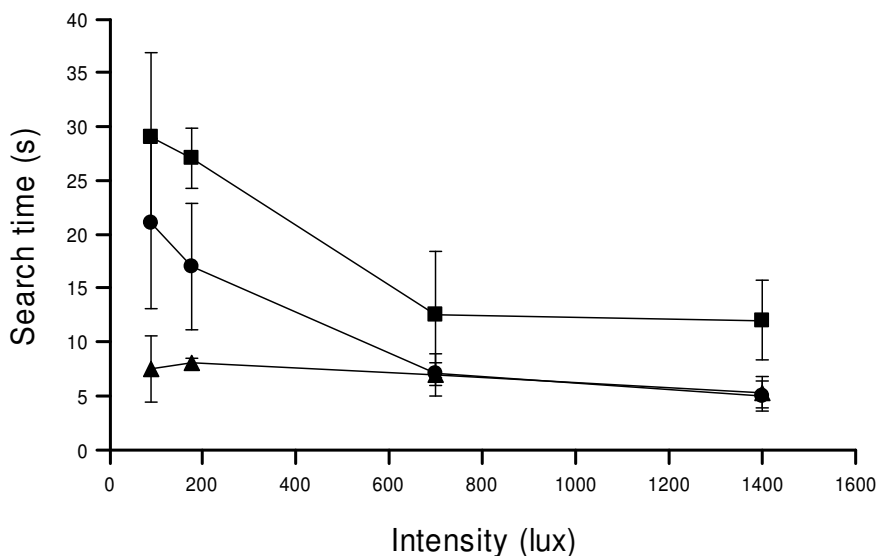


Figure 2. Search time for small, but not large, flowers depends on illumination intensity. Individual bumblebees were tested three times at each light condition in a random order in a flight arena. Search time (\pm SD; $N = 5$ bees) was measured at four different light intensities. Squares, 8 mm flower diameter; Circles, 15 mm flower diameter; triangles, 28 mm flower diameter.

Search times for large flowers ($\varnothing = 28$ mm) were only marginally affected by light intensity (Figure 2). For medium ($\varnothing = 15$ mm) and small flower sizes ($\varnothing = 8$ mm), however, search times increased by a factor of 2–3 as intensity was reduced from 700 to 88 lux. This means that light intensity levels, even during diurnal foraging, can very severely constrain foraging efficiency.

Chromatic and Achromatic Search Strategies

Bees have color vision, which they can use for target detections (in which case detectability will depend on color contrast between the object and its background), or they can use the achromatic contrast an object makes with its background (Giurfa & Lehrer, 2001). To detect color contrast an animal needs at least two different color receptor types. Most species of bee have three, which are most sensitive in the UV, blue and green parts of the spectrum (Briscoe & Chittka, 2001; Peitsch et al., 1992). Color contrast must depend on neural computations that evaluate the differences between signals from these different color receptor types. Although the details of the neural processing of chromatic information in the bee brain are still rather sketchy, there is widespread agreement that at least two color opponent processes are involved, which compare signals from different color receptor types (Backhaus, 1991; Chittka, Beier, Hertel, Steinmann, & Menzel, 1992;

Chittka & Brockmann, 2005; Lotto & Chittka, 2005). On this basis, and given the spectral sensitivities of the color receptors involved, it is possible to accurately predict color differences in the perceptual “color space” of the organism in question (Chittka, 1992; Chittka & Brockmann, 2005), with excellent agreement between the predictions of the model and behavioral data (Chittka et al., 1992). Such a model also allows us to design color stimuli so as to systematically vary color contrast under controlled laboratory conditions.

We tested the ability of bumblebees to find artificial flowers, designed to vary systematically in the color contrast they offered against a green background. As would be expected if bees were using color vision for target detection, we found that for large artificial flowers, search time was negatively correlated with color contrast: target flowers that contrasted less in color with their background took longer to find (Figure 3; Spaethe et al., 2001).

Behavioral data indicate that the spatial resolution of the color vision system in bees is considerably worse than the theoretical limit set by interommatidial angle (see above). In order for an object to be identified by color, it needs to subtend a visual angle of at least 15° (Giurfa & Lehrer, 2001). However, bees can still identify smaller targets (down to a visual angle of 5°), but the visual inputs are based purely on differences in green receptor signals across the ommatidial array. Thus, there are parallel channels in the bee’s visual system: a lower resolution chromatic (color contrast) channel, and a higher resolution achromatic (green contrast) one.

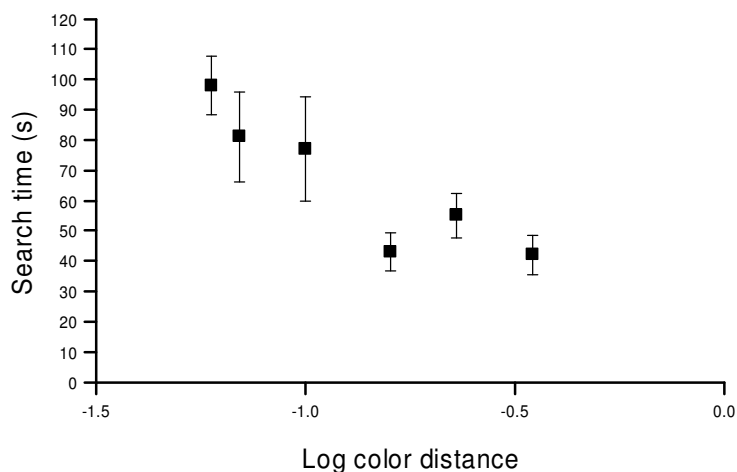


Figure 3. Search time is negatively correlated with floral color contrast against background ($r_s = -0.83$; $N = 6$; $p < 0.05$). Color loci of artificial flowers and a green background were plotted in a bumblebee chromaticity diagram to calculate flower-background color distance (for full details see Spaethe et al. 2001). Search time (\pm SD) was measured as the time elapsed from entering the arena to landing on the 3rd chip, excluding time spent on flowers. Three artificial flowers ($\varnothing = 28$ mm) were placed in a flight arena at random positions similar to the experiments of Figures 1 and 2.

In keeping with this, the correlation between color contrast and search time disappears as flower diameter is reduced from 28 to 15 mm, and search time for small targets is highly correlated with the achromatic (green) contrast the flower makes with its background (Spaethe et al., 2001). This raises an additional ques-

tion, however. Since the bee's visual system cannot identify the color of a target until it subtends an angle $> 15^\circ$, and choice behavior for targets subtending angles between 15° and 5° is governed by green contrast, then detectability should always be correlated with green contrast: as a bee approaches a flower, that flower will inevitably exceed the 5° threshold before the 15° threshold. Identification by color should always be subsequent to detection by green contrast.

Nevertheless, our results show that bees do use color contrast to detect large flowers (Spaethe et al., 2001). It may be that an additional strategy is involved, whereby bees may be selectively using color contrast when they expect large flowers, and they ignore the signal from the green receptor channel. This may enable bees to identify flowers with more certainty, simply because color contrast uses three input variables, whereas green contrast is only defined by one. Thus, bees face a tradeoff between reliable identification and rapid detection, and the relative benefits of both may change depending on floral size.

Bumblebees do indeed seem to use different flight strategies depending on target size. When searching for small targets, bumblebees change their flight behavior in several ways. They fly significantly slower and closer to the ground, thus increasing the minimum detectable area subtended by an object on the ground (Figure 4). In addition, they use a different neuronal channel for flower detection: instead of color contrast, they now employ only the green receptor signal for detection (Spaethe et al., 2001). Can we relate these behavior changes to temporal limitations of the two different neuronal channels involved in stimulus detection and recognition, color vision and green contrast analysis? During flight in a natural foraging bout, temporal constraints of the respective neuronal channels become relevant for the detection process. As a bee moves across a meadow with flowers, the contrast each flower makes with its background is reduced, and spatial resolution also decreases (Srinivasan & Lehrer, 1984). With increasing flight speed, the amount of time a flower passes through the receptive field of a visuo-neuronal channel is reduced. Beyond a critical speed, this time window may be too short to be resolved by the temporal sensitivity of a receptor or neuronal channel, and the bee may fail to detect the object. In experiments with flickering stimuli, Srinivasan and Lehrer (1984) concluded that a bee needs 10 ms to compute the color of an object. The green receptor channel, which also drives the bees' optomotor response, has been reported to have about half that integration time, which appears to be close to the photoreceptors' temporal resolution (Autrum & Stoecker, 1950). Spaethe et al. (2001) demonstrated that the changes in flight height and speed can be explained precisely by these temporal limitations of color vision and "green vision": bumblebees adjust their flight behavior to facilitate target detection; for example, bees slow down just sufficiently to minimize the risk of missing targets when using color vision, and when objects are so small that they would fall below the 10 ms threshold of the color channel, bees resort to using the achromatic green channel, which is less precise (in terms of object identification) but faster.

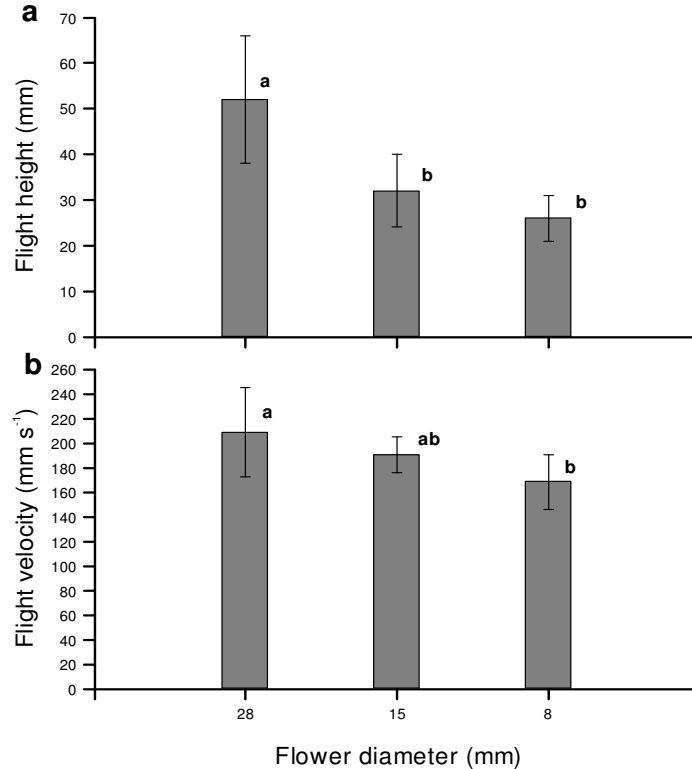


Figure 4. Bumblebees adjust flight height (a) and flight velocity (b) to match flower size. (Wilcoxon test; differences are significant where letters are different; Mean \pm SD; $N = 7$; for experimental details, see Spaethe et al. 2001).

Parallel or Serial Processing in Bee Visual Search?

An insect searching a meadow for flowers may detect several flowers from different species per second (Chittka et al., 1999), so the task of choosing the right flowers rapidly is not trivial. In human visual search, selecting a target from a range of distractor stimuli can be very rapid provided stimuli vary along only a single dimension (e.g., they all have the same shape, but differ in color). In such cases, the presented stimuli are examined in parallel and the target is said to "pop out." In this situation search time is relatively fast and constant; there is no increase in search time with increasing number of distractors (McElree & Carrasco, 1999; Nakayama & Silverman, 1986). The search is said to be parallel. If, however, targets and stimuli vary along more than a single dimension (e.g., color and shape), each stimulus is examined in series (serial search) and reaction times now increase drastically with the number of distractors.

The limits in spatial resolution of the bee visual system, discussed above, imply that parallel search in insects would not be possible unless the approach was close enough to exceed the visual threshold angle needed to detect objects, either by green contrast, or by color contrast. Nevertheless, since the issue of whether serial or parallel visual search is used in foraging insects has not yet been addressed, we have recently begun to investigate this question in honeybees. Individ-

ual bees were trained to choose a colored disc (target) among a varying number of different-colored discs (distractors), which were presented simultaneously on a square board (Spaethe, Tautz, & Chittka, 2006). The experiment was arranged so that the square array (4x4) of discs would have subtended a visual angle of $65^\circ \times 65^\circ$ at the position where the bee was first confronted with the choice array. Individual discs subtended an angle between 12.5° (for targets in the corners of the array) and 15° (for central targets). We measured accuracy (proportion of correct choices) and decision time (time between target detection and choice) as a function of distractor number (one, three, eight or fifteen) and color. Three color combinations were tested: (1) blue target and yellow distractors; (2) yellow target and blue distractors; and (3) yellow targets and mixed colored distractors. The results showed that there seems to be no “pop out” effect in bees, which would be characteristic of parallel search. Instead, for all color combinations, we found a significant increase in decision time and a significant decrease in accuracy with increasing distractor number. Increasing distractor number from 1 to 15 increases decision time approximately 1.5-fold, and increases error rate four-fold (Figure 5). Note that flights to distractors were not exploratory behavior, but genuine errors: bees never terminated such flights with a landing, and always aborted their flight shortly before making contact. The linear increase of decision time with distractor number is characteristic of serial search in humans (i.e., there is no “pop out” effect). We therefore conclude that, even when stimuli differ in only one stimulus dimension, and are present in the visual field in such a way that parallel search would theoretically be possible, visual search in bees is nevertheless serial, whereas such searches would be parallel in humans (Nakayama & Silverman, 1986).

Interestingly, although bees were able to detect and choose a target regardless of its position in the target-distractor array, speed and accuracy were not homogeneous across the visual field. We found that search was most accurate when the target was presented in the ventral part and least accurate when it was presented in the most dorsal part of the visual field (Figure 6). All error rates were significantly lower than the expected error rate when the search was completely random (94%). These differences cannot simply be explained by the slight variations in the visual angle of the target at different positions in the visual field. The visual angle would have been largest for targets in the centre, for example, but error rates here were approximately 3 times higher than for ventral targets, which would have presented a slightly smaller visual angle. Moreover, error rate was almost 5 times higher when the target was presented in the most dorsal row compared to when the target was presented in the ventral row, but visual angles for target positions in both rows are identical (Figure 6).

Earlier investigations, where bees had to identify single visual patterns, also revealed a better performance in the ventral part of the visual field (Chittka, Hoffmann, & Menzel, 1988; Giurfa et al., 1999; Lehrer, 1997; Menzel & Lieke, 1983). Since there is no corresponding asymmetry in the ommatidial array of the compound eye that explains this dorsoventral asymmetry in performance (Lehrer, 1999), the explanation presumably depends on post-receptoral neural processing. For example, second or higher-order optic lobe neurons receiving input from dorsal ommatidia might have larger receptive fields than more ventral ones. It is equally possible that bees allocate their attention non-uniformly across their visual field but focus attention naturally to the frontal ventral region. A potential test to

distinguish between both hypotheses might be the use of a pre-cue, which draws attention to the dorsal part of the visual field (Tsal, 1983). In humans, attention can be drawn to a specific point within the visual field when a pre-cue (for instance a small dot) is presented at this position shortly prior to when target and distractors are presented. Reaction time and accuracy decline when the target is presented further away from the pre-cued position (Tsal, 1983). Such experiments might help distinguish between the two possibilities for explaining the dorsoventral asymmetry in the visual field (i.e., hardwired, peripheral neuronal circuitry vs. a more dynamic attentional mechanism).

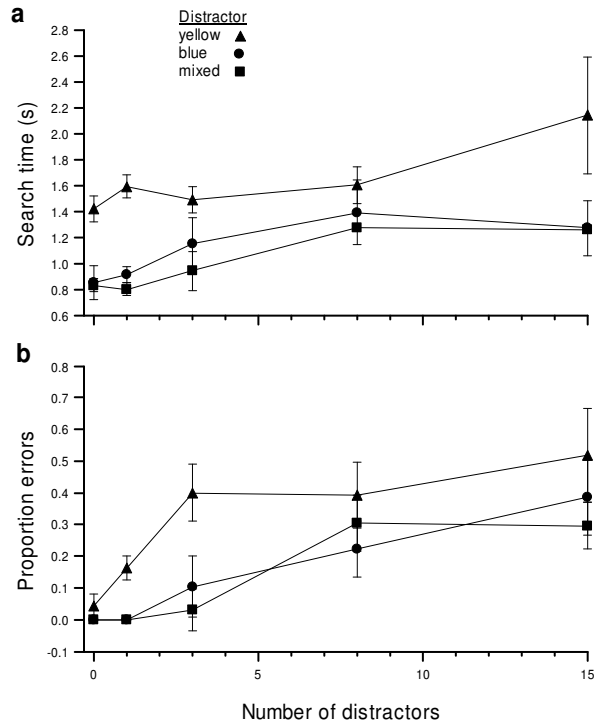


Figure 5. Search times and error rates of honeybees searching for a target depend on the number simultaneously presented distractors. Bees were trained to enter an experimental box (0.43 m · 0.43 m · 0.3 m) by passing a small hole and fly to a colored circular target on a green back wall of the box to receive a sucrose reward. After each foraging bout the target was randomly mounted at one of 16 (4 x 4) possible positions at the back wall. During experiments the rewarded target was presented together with non-rewarding distractors of the same size but different colors. When bees searched for a blue target, a varied number (0, 1, 3, 8 or 15) of yellow distractors were offered, and when they searched for a yellow target, the distractors were either blue in one experiment or of mixed colors in a second experiment. Each bee was filmed by a digital camera from above and bees' accuracy as well as flight time between entering the box and approaching the target or distractor was recorded (\pm SE; $N = 5$) (for more details see Spaethe et al. 2006).

Speed-accuracy Tradeoffs

Improved accuracy in solving discrimination tasks comes at a cost in response time; if subjects are forced to make rapid decisions, accuracy will suffer. Research with humans shows that there is a tight relationship between choice speed and accuracy (Zenger & Fahle, 1997), but such speed-accuracy tradeoffs have only recently come under scrutiny in insect vision. In an experiment involv-

ing “virtual flowers” projected by a data projector onto the transparent wall of a flight arena, bumblebees were trained between two very similar types of flowers (Chittka et al., 2003), and their choice accuracy as well as decision speed was quantified.

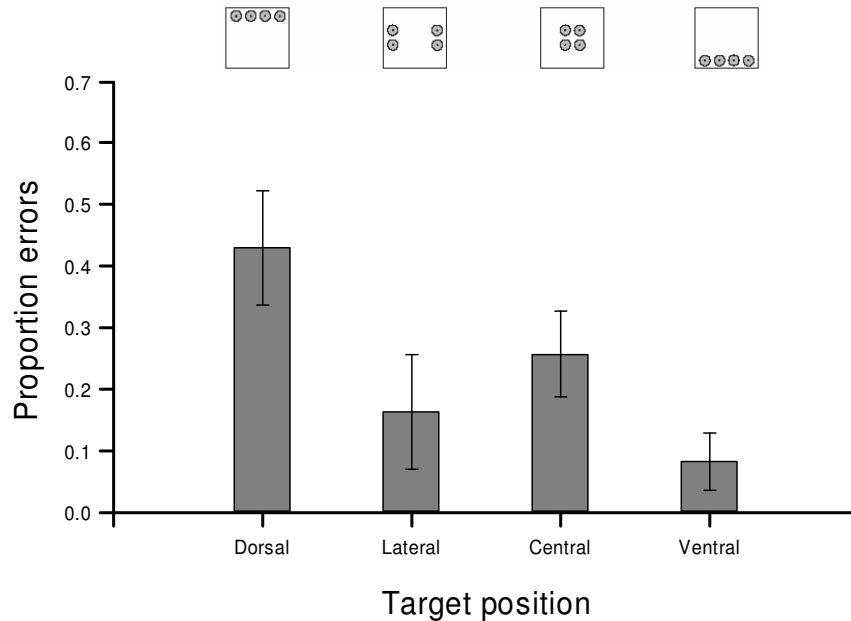


Figure 6. Error rate varies with target position. Targets and distractors were arranged to appear in the dorsal, lateral, central or ventral portions of the visual field (insets). Error rate (\pm SE; $N=5$) was measured as the proportion of flights to target that crossed a criterion decision line 5 cm from the target array.

There were pronounced differences between individual bees’ strategies: there was a strong correlation between decision time and accuracy (Figure 7). The more time an individual bee invested, the more accurate her choices. Bees that made rapid choices were also more error-prone. We then introduced higher costs to making errors, by penalizing incorrect choices with aversive quinine solution. Under these conditions, all bees improved their accuracy significantly. This was the first demonstration of between-individual and within-individual speed-accuracy tradeoffs in an insect (Chittka et al., 2003). Such speed accuracy tradeoffs in visual search are not, however, found in all conditions. Dyer and Chittka (2004b) recently showed that between-individual speed accuracy tradeoffs only occur when colors are very similar, but not for clearly distinguishable colors. They also showed that bees need more time to solve difficult color discrimination tasks, where targets and distractors are highly similar.

Can an Insect’s Decisions Be Informed by Estimations of Time and Rate?

If bees can flexibly alternate search strategies between accuracy and speed, this implies that the time interval taken to complete a task is a significant variable. But can bees actually measure time intervals? The implication is certainly widespread.

According to optimal foraging theory, for example, an insect might measure flower profitability by assessing nectar gained per unit time (Chittka, Ings, & Raine, 2004; Schilman & Roces, 2003), and cost in terms of flower handling time (Saleh, Ohashi, Thomson, & Chittka, 2006). The assumption that insects can measure time (or its reciprocal, rate) is also implicit in studies on insect flight speed and distance measurement (Chittka & Tautz, 2003; Srinivasan, Zhang, Altwein, & Tautz, 2000). All of these studies suggest that (at least some) foraging insects can measure time (or rate).

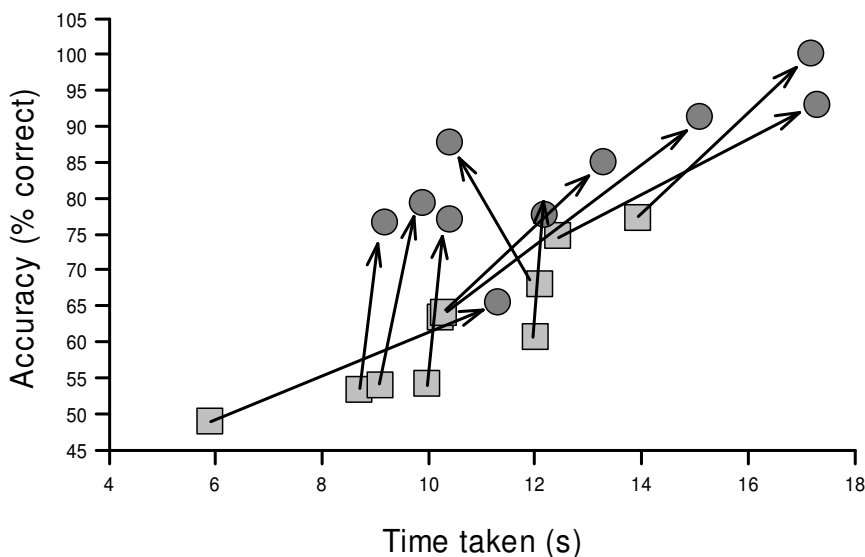


Figure 7. Accuracy of discrimination between two virtual flowers of similar color is correlated with time taken to make the choice. Each symbol denotes average performance of one individual bee under one experimental condition. Black symbols: targets are rewarded with sucrose solution, while distractors contain no reward (plain water). Bees which invest more time make more accurate choices. When distractors are penalized with bitter quinine solution (gray symbols), all bees improve in accuracy, and 9 of 10 bees invest more time to do so. Only in 5 bees does this investment appear substantial, however: 4 bees appear to increase accuracy with relatively marginal increases in decision time. Arrows link the average values for individual bees under the two experimental conditions (for more details see Chittka et al., 2003).

Although it has long been known that insects have circadian clocks (Stanewsky, 2003), which allow them to modify their behavior in accordance with relatively fixed and regularly repeating temporal cycles (even, in the case of bees, allowing them to schedule their flowers-visits to specific times of the day), until recently there has been no direct evidence that insects can sense the passage of relatively short and inherently variable intervals of time that are contingent on their own behavior.

In another example of a fruitful application of concepts and methodologies from the vertebrate experimental psychology literature to the behavioral analysis of foraging insects, Boisvert and Sherry (2006) adopted a standard fixed interval procedure to probe the interval timing capacity of bumblebees. A bumblebee was first trained to obtain a sugar reward by inserting its proboscis through a small hole in the wall of an experimental chamber. During experimental sessions, a fixed time interval was introduced between the initial cue (illumination of the experimental

chamber) and availability of reward. Responses by the bee (proboscis extension) during this fixed interval were without effect, but the first response after elapse of the interval triggered sucrose reward. When rats or pigeons are trained with similar procedures, the animals soon learn about the time delay involved, and then typically withhold their response for the first part of the fixed interval (Gallistel & Gibbon, 2000).

Bumblebees behaved in a similar manner. When trained on fixed intervals of either 12 or 24 s, responses were delayed appropriately. The delay from the beginning of the timed interval to the first response (wait time) was significantly longer for the 24 s than for the 12 s intervals. However, in both cases, mean wait times accounted for about 1/3 of the interval duration, and the maximal rate of responding occurred at or near the end of the time interval. The bees, therefore, could predict the anticipated end of the interval and delay their responses accordingly. There is much still to be done before we can compare the interval timing capacities of bees with those of higher vertebrates. Nevertheless, this important result provides direct evidence that bees can estimate the shorter, variable time intervals that are not locked to circadian rhythms, and this capacity may be vital in selecting behavioral strategies in a variety of real-world contexts.

Interestingly, studies from the vertebrate experimental psychology literature suggest there may be commonalities in the representation of time and quantity, and specifically, numerosity, or countable quantity (Gallistel & Gelman, 2000). The reciprocal of time is rate, and rate is quantity over time. Returning to the context of a foraging insect, selecting strategies to optimize foraging efficiency requires information about duration and quantity, and probably also countable quantity or numerosity. Crop distension, for example, is a non-countable quantity, but quantity of flowers visited is countable. The two together provide useful information concerning flower profitability. Similarly, velocity is distance over time, and distance is formally non-countable. However, to be able to estimate speed at any one time may require attending to discrete (countable) cues. In studies of bee odometry under laboratory conditions discrete visual cues are required (Chittka & Tautz, 2003; Srinivasan et al., 2000), and there is also evidence that the searching behavior of bees and ants can be modulated in a predictable way by countable quantity (Chittka & Geiger, 1995; Wittlinger, Wehner, & Wolf, 2006). Taken together the studies reviewed in this section are highly suggestive that information about time, rate and numerosity can inform insects' decisions about search strategies.

Conclusion

It is easy to underestimate the complexity of the task faced by a flower visiting insect. Rewarding flowers may have to be identified and selected from dozens of species on offer, all of which may be encountered in rapid succession. The cognitive capacities of such insects, which have evolved to help them in this task, are correspondingly impressive (Collett et al., 1993; Dyer, Neumeyer, & Chittka, 2005; Giurfa, 2003; Menzel & Giurfa, 2001; Srinivasan et al., 1993). Although the accuracy with which visual discriminations can be made has been the subject of much research, one of our major aims here has been to show that accuracy is tightly (but flexibly) interlinked with speed. We hope to have demonstrated that

decision speed is an important factor that needs to be evaluated in conjunction with accuracy in animal choice tests. In other words, accuracy (at the behavioral level) is not a fixed parameter of the visual system in question, but depends instead on the behavioral context. In many psychophysical experiments on insects, accuracy in discrimination tests has been used to support inferences about the underlying neuronal mechanisms (Horridge, 2000; Vorobyev, Brandt, Peitsch, Laughlin, & Menzel, 2001), but behavioral accuracy depends on a variety of stimulus properties, as well as sensory and cognitive limitations (see also Dyer & Neumeyer, 2005). Importantly, we also demonstrate that choice accuracy depends strongly on motivation: whether or not reward is combined with punishment. This implies that the limits of discrimination may easily be underestimated. Unless emphasis on either speed or accuracy is clearly defined, results may be difficult to interpret, and conclusions about neuronal mechanisms ambiguous. However, it should be possible to avoid such pitfalls if response time is always measured in experiments where discrimination accuracy is quantified (which would allow the possibility of speed-accuracy tradeoffs to be evaluated). We also emphasize here the “individuality” of insects: contrary to the common notion of insects as mass-produced replicas of one another, sacrificing the cognitive flexibility required for experience-dependent adaptability of behavior in favour of brief lives, exuberant reproduction and hard-wired behavior programs, we show here that they possess considerable flexibility, and that there is genuine variation in the strategies by which individual insects solve foraging problems, including how they allocate time to make difficult judgments. Finally, an important question that has only just begun to be directly addressed concerns how insects actually estimate the duration of time intervals (Boisvert & Sherry, 2006; Skorupski & Chittka, 2006), since this would seem crucial to their ability to flexibly emphasize either accuracy or speed in their behavioral decisions.

References

- Autrum, H. J., & Stoecker, M. (1950). Die Verschmelzungsfrequenzen des Bienenauges. *Zeitschrift fuer Naturforschung*, **5**, 38-43.
- Backhaus, W. (1991). Color opponent coding in the visual-system of the honeybee. *Vision Research*, **31**, 1381-1397.
- Benard, J., Stach, S., & Giurfa, M. (2006). Categorization of visual stimuli in the honeybee *Apis mellifera*. *Animal Cognition*, **9**, 257-270.
- Boisvert, M. J., & Sherry, D. F. (2006). Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. *Current Biology*, **16**, 1636-1640.
- Briscoe, A. D., & Chittka, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology*, **46**, 471-510.
- Chittka, L. (1992). The color hexagon: A chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *Journal of Comparative Physiology A*, **170**, 533-543.
- Chittka, L., Beier, W., Hertel, H., Steinmann, E., & Menzel, R. (1992). Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in hymenoptera. *Journal of Comparative Physiology A*, **170**, 545-563.
- Chittka, L., & Brockmann, A. (2005). Perception space - The final frontier. *PLOS Biology*, **3**, 137.
- Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for accuracy. *Nature*, **424**, 388-388.

- Chittka, L., & Geiger, K. (1995). Can honey bees count landmarks? *Animal Behaviour*, **49**, 159-164.
- Chittka, L., Hoffmann, M., & Menzel, R. (1988). Discrimination of UV-green patterns in honey bees. In N. Elsner & F. G. Barth (Eds.), *Sense organs* (pp. 218). Stuttgart, Germany: Thieme.
- Chittka, L., Ings, T. C., & Raine, N. E. (2004). Chance and adaptation in the evolution of island bumblebee behaviour. *Population Ecology*, **46**, 243-251.
- Chittka, L., Shmida, A., Troje, N., & Menzel, R. (1994). Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. *Vision Research*, **34**, 1489-1508.
- Chittka, L., & Tautz, J. (2003). The spectral input to honeybee visual odometry. *Journal of Experimental Biology*, **206**, 2393-2397.
- Chittka, L., Thomson, J. D., & Waser, N. M. (1999). Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften*, **86**, 361-377.
- Collett, T. S., Fry, S. N., & Wehner, R. (1993). Sequence learning by honeybees. *Journal of Comparative Physiology A*, **172**, 693-706.
- Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London B*, **353**, 1245-1255.
- Downing, C. J., & Pinker, S. (1985). The spatial structure of visual attention. In M. J. Posner & O. S. M. Martin (Eds.), *Attention and performance* (Vol. 11, pp. 171-187). Hillsdale, NJ: Erlbaum.
- Dyer, A. G., & Chittka, L. (2004a). Biological significance of discriminating between similar colours in spectrally variable illumination: Bumblebees as a study case. *Journal of Comparative Physiology A*, **190**, 105-114.
- Dyer, A. G., & Chittka, L. (2004b). Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *Journal of Comparative Physiology A*, **190**, 759-763.
- Dyer, A. G., & Neumeyer, C. (2005). Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *Journal of Comparative Physiology A*, **191**, 547-557.
- Dyer, A. G., Neumeyer, C., & Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognize images of human faces. *Journal of Experimental Biology*, **208**, 4709-4714.
- Frisch, K. v. (1967). *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.
- Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, **4**, 59-65.
- Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review*, **107**, 289-344.
- Giurfa, M. (2003). The amazing mini-brain: Lessons from the honeybee. *Bee World*, **84**, 5-18.
- Giurfa, M., Hammer, M., Stach, S., Stollhoff, N., Muller-Deisig, N., & Mizyrycki, C. (1999). Pattern learning by honeybees: Conditioning procedure and recognition strategy. *Animal Behaviour*, **57**, 315-324.
- Giurfa, M., & Lehrer, M. (2001). Honeybee vision and floral displays: From detection to close-up recognition. In L. Chittka & J. D. Thomson (Eds.), *Cognitive ecology of pollination* (pp. 61-82). Cambridge, UK: Cambridge University Press.
- Gould, J. L. (1985). How bees remember flower shapes. *Science*, **227**, 1492-1494.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Berlin, Germany: Springer.
- Horrige, A. (2000). Seven experiments on pattern vision of the honeybee, with a model. *Vision Research*, **40**, 2589-2603.

- Jander, U., & Jander, R. (2002). Allometry and resolution of bee eyes (Apoidea). *Arthropod Structure & Development*, **30**, 179-193.
- Kelber, A., Balkenius, A., & Warrant, E. J. (2002). Scotopic colour vision in nocturnal hawkmoths. *Nature*, 419, 922-925.
- Kemp, D. J. (2002). Visual mate-searching behaviour in the evening brown butterfly, *Melanitis leda* (L.) (Lepidoptera : Nymphalidae). *Australian Journal of Entomology*, **41**, 300-305.
- Land, M. F. (1999). Compound eye structure: matching eye to environment. In S. N. Archer (Ed.), *Adaptive mechanisms in the ecology of vision* (pp. 51-71). Norwell, MA: Kluwer Academic Publishers.
- Laughlin, S. B. (1981). Neural principles in the peripheral visual systems of invertebrates. In H. Autrum (Ed.), *Comparative physiology and evolution of vision in invertebrates. B: Invertebrate visual centers and behavior I*, Vol. VII/6B (pp. 133-280). Berlin, Germany: Springer.
- Lehrer, M. (1997). Honeybee's use of spatial parameters for flower discrimination. *Israeli Journal of Plant Sciences*, **45**, 157-167.
- Lehrer, M. (1999). Dorsoventral asymmetry of colour discrimination in bees. *Journal of Comparative Physiology A*, **184**, 195-206.
- Lotto, R. B., & Chittka, L. (2005). Seeing the light: Illumination as a contextual cue to color choice behavior in bumblebees. *Proceedings of the National Academy of Sciences U.S.A.*, 102, 3852-3856.
- McElree, B., & Carrasco, M. (1999). The temporal dynamics of visual search: Evidence for parallel processing in feature and conjunction searches. *Journal of Experimental Psychology: Human Perception and Performance*, **25**, 1517-1539.
- Menzel, R. (2001). Behavioral and neural mechanisms of learning and memory as determinants of flower constancy. In L. Chittka & J. D. Thomson (Eds.), *Cognitive ecology of pollination* (pp. 21-40). Cambridge, UK: Cambridge University Press.
- Menzel, R., & Giurfa, M. (2001). Cognitive architecture of a mini-brain: The honeybee. *Trends in Cognitive Sciences*, **2**, 62-71.
- Menzel, R., & Lieke, E. (1983). Antagonistic color effects in spatial vision of honeybees. *Journal of Comparative Physiology A*, **151**, 441-448.
- Nakayama, K., & Silverman, G. H. (1986). Serial and parallel processing of visual feature conjunctions. *Nature*, **320**, 264-265.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F., & Menzel, R. (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A*, **170**, 23-40.
- Saleh, N., Ohashi, K., Thomson, J. D., & Chittka, L. (2006). Facultative use of repellent scent marks in foraging bumblebees: Complex versus simple flowers. *Animal Behaviour*, **71**, 847-854.
- Schilman, P. E., & Roces, F. (2003). Assessment of nectar flow rate and memory for patch quality in the ant *Camponotus rufipes*. *Animal Behaviour*, **66**, 687-693.
- Seeley, T. D. (1995). *The wisdom of the hive*. Cambridge, MA: Harvard University Press.
- Skorupski, P., & Chittka, L. (2006). Animal cognition: An insect's sense of time? *Current Biology*, **16**, R851-R853.
- Spaethe, J., Tautz, J., & Chittka, L. (2001). Visual constraints in foraging bumblebees: Flower size and color affect search time and flight behavior. *Proceedings of the National Academy of Sciences U.S.A.*, **98**, 3898-3903.
- Spaethe, J., Tautz, J., & Chittka, L. (2006). Do honeybees detect colour targets using serial or parallel visual search? *Journal of Experimental Biology*, **209**, 987-993.
- Srinivasan, M. V., & Lehrer, M. (1984). Temporal acuity of honeybee vision: Behavioural studies using moving stimuli. *Journal of Comparative Physiology A*, **155**, 297-312.

- Srinivasan, M. V., Zhang, S., Altwein, M., & Tautz, J. (2000). Honeybee navigation: nature and calibration of the "odometer." *Science*, **287**, 851-853.
- Srinivasan, M. V., Zhang, S. W. and Rolfe, B. (1993). Pattern vision in insects: "Cortical" Processing? *Nature*, **362**, 539 - 540.
- Stanewsky, R. (2003). Genetic analysis of the circadian system in *Drosophila melanogaster* and mammals. *Journal of Neurobiology*, **54**, 111-147.
- Theobald, J. C., Greiner, B., Wcislo, W. T., & Warrant, E. J. (2006). Visual summation in night-flying sweat bees: A theoretical study. *Vision Research*, **46**, 2298-2309.
- Treisman, A., & Gormican, S. (1988). Feature analysis in early vision: evidence from search asymmetries. *Psychological Review*, **95**, 15-48.
- Tsal, Y. (1983). Movements of attention across the visual field. *Journal of Experimental Psychology: Human Perception and Performance*, **9**, 523-530.
- Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S. B., & Menzel, R. (2001). Colour thresholds and receptor noise: behaviour and physiology compared. *Vision Research*, **41**, 639-653.
- Williamson, S. J., & Cummins, H. Z. (1983). *Light and color in nature and art*. New York: Wiley.
- Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: Stepping on stilts and stumps. *Science*, **312**, 1965-1967.
- Wolfe, J. M. (1999). How do you pay attention? *Nature*, **400**, 813-815.
- Zenger, B., & Fahle, M. (1997). Missed targets are more frequent than false alarms: A model for error rates in visual search. *Journal of Experimental Psychology*, **23**, 1783-1791.