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Dissociation of visual localization and visual detection in rhesus monkeys (*Macaca mulatta*)

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Abstract

Conscious and unconscious cognitive processes contribute independently to human behavior and can be dissociated. For example, humans report failing to see objects clearly in the periphery while simultaneously being able to grasp those objects accurately (Milner in Proc R Soc B Biol Sci 279:2289–2298, 2012). Knowing whether similar dissociations are present in nonverbal species is critical to our understanding of comparative psychology and the evolution of brains. However, such dissociations are difficult to detect in nonhumans because verbal reports of experience are the main way we discriminate putative conscious from unconscious processing. We trained monkeys in a *localization* task in which they responded to the location where a target appeared, and a matched *detection* task in which they reported the presence or absence of the same target. We used masking to manipulate the visibility of targets. Accuracy was high in both tasks when stimuli were unmasked and was attenuated by visual masking. At the strongest level of masking, performance in the detection task was at chance, while localization remained significantly above chance. Critically, errors in the detection task were predominantly misses, indicating that the monkeys' behavior remained under stimulus control, but that the monkeys did not detect the target despite above-chance localization. While these results cannot establish the existence of phenomenal vision in monkeys, the dissociation of visually guided action from detection parallels the dissociation of conscious and unconscious vision seen in humans.

Keywords

Blindsight; Masking; Signal detection; Perception; Vision

Introduction

The sensory systems of primates are bombarded with information, much more than can be processed in depth. Sensory overload can be avoided by ignoring irrelevant stimuli (Desimone and Duncan 1995) or by channeling information into independent processing streams, some of which can generate behavior without taxing limited attentional resources (Goodale and Milner 1992). In humans, some sensory stimuli can control behavior even when they do not produce phenomenal percepts (Engel and Singer 2008; Neumann 1990). For example, we can accurately grasp objects in the visual periphery with precision that greatly exceeds visual discrimination in the same region (Goodale and Murphy 1997), and visual primes affect reaction times in number-identification tasks even when such primes are not consciously perceived (Naccache et al. 2002). Evidence from patients with brain damage also dissociates phenomenal perception and action. In blind-sight, patients with damage to primary visual cortex appear not to experience visual perception in the affected visual areas, but nonetheless maintain some ability to localize objects, detect movement, grasp accurately, and avoid obstacles (Weiskrantz 1990). Similarly, patients with damage in the ventral visual processing stream have been reported to have severe impairments in conscious visual perception, but largely intact visually guided action (Goodale and Milner 2004).

While it is more difficult to convincingly dissociate phenomenal or conscious perception from action in non-verbal species, there is some evidence for corresponding phenomena in other primates. Cowey and Stoerig (1997) tested monkeys with unilateral lesions in primary visual cortex. The monkeys learned to accurately localize targets in both the affected and normal visual fields in forced-choice tests. In other training, monkeys learned to make a specific response on blank trials on which no stimulus was presented. On intermixed trials, when a stimulus did appear, the correct response was to localize the stimulus. Instead, monkeys made the “blank trial” response when to-be-localized stimuli appeared in the affected field. That targets presented in the affected field supported accurate localization without apparent detection creates an intriguing parallel with the behavior observed in humans with blindsight due to brain damage. However, this parallel between human and nonhuman primate visual processing is still limited because we do not know whether visual detection and visual localization can be reliably dissociated in normal intact monkeys, as in normal humans. Additionally, the onset of primary visual cortex (V1) lesions in monkeys is followed by extensive degeneration of visual circuits synapsing in the lateral geniculate (LGN), probably fundamentally altering the transmission of visual signals to secondary (extrastriate) visual areas responsible for residual visual function (Leopold 2012). Here, we address the need for studies contrasting visual detection and localization in normal monkeys with our report of a new dissociation of visually guided action and perception. We used techniques that closely parallel those that have been used in normal humans, providing an especially direct comparison between humans and monkeys.

Visual masking is an excellent method for contrasting localization and detection of visual stimuli. Parametric manipulations of the timing and duration of visual targets and masks result in systematic changes in the ease with which visual targets are processed (Dehaene et al. 1998; Fahrenfort et al. 2007; Fehrer and Raab 1962; Klotz and Neumann 1999). In our implementation, masks followed immediately after the offset of targets and made the targets

less perceptible than would be the case without the masks. The interval between the onset of the target and the onset of the mask is called the stimulus onset asynchrony (SOA) and is a major determinant of the efficacy of masking (Breitmeyer and Ömen 2006). Masking has been shown to affect the detectability of targets in monkeys with simultaneous neural recordings, indicating that masking interrupts visual processing of targets in the ventral visual processing stream (Kovács et al. 1995; Lamme et al. 2002). In the present research, we tested whether interrupting visual processing using such masks affects detection independently of localization.

We trained monkeys in a short-latency, highly stereotyped localization task, in which they had to touch one of the four locations after a target had been presented. We also trained them in a detection task, using identical stimuli, in which they had to report whether or not a target had been presented by pressing one of the two buttons. Visual masks were used, and the SOA manipulated to parametrically attenuate processing of the targets. We hypothesized that if visually guided action and visual perception occurred independently, then monkeys should be able to accurately localize targets that they were not able to detect.

Experiment 1: Localization of masked stimuli

Methods

Five adults (mean age = 7.9 years), male rhesus monkeys (*Macaca mulatta*), were tested. The monkeys were mother-reared in large social groups until they were approximately 2.5 years of age and then housed in socially compatible pairs in the laboratory. Monkeys were experienced in automated cognitive testing, but not with the tasks used in this study. Fifteen-inch (38 cm) LCD color touch screen monitors with acoustic pulse recognition (ELO, Menlo Park, CA, USA) were attached to the monkeys' home cages such that they could be tested in their home environment. The monitors ran at a refresh rate of 60 Hz with a resolution of $1,024 \times 768$ pixels. Generic stereo speakers and automated food dispensers (Med Associates, Inc., St. Albans, VT, USA) were used to signal and administer rewards. Food cups were located below the touch screens. Nutritionally balanced pellets (Bio-Serv, Frenchtown, NJ, USA) were used as rewards. Sessions were conducted between 11:00 AM and 5:00 PM, 6 days a week. No fixation mechanisms were used to restrain the monkeys, and therefore, the sizes of stimuli (see below) could not be stated in visual angle.

Localization trials began with the presentation of a green "ready" square (100 pixels, i.e., 7.3 cm, square). Monkeys initiated trials at their own pace by touching the square twice. After an interval of 500 ms, a gray target circle (35 pixels, 1.0 cm, in diameter) appeared in one of the four corners of the screen, chosen according to a pseudorandom schedule that ensured counterbalancing. Exactly at the offset of the target, four identical annuli (inner diameter 35 pixels, 1.0 cm; outer diameter 77 pixels, 2.2 cm) appeared, serving both as masks and as response buttons. The inner contours of the annuli exactly matched the outer contours of the target circle, making them function as meta-contrast masks (van Gaal et al. 2008). Targets were more similar in luminance to the background than to the masks, causing targets and masks to have low and high contrasts, respectively. This was expected to reduce the visibility of the targets monotonically as the target-mask SOAs were made shorter (Francis

1997). All stimuli were presented on a gray square (length and height 500 pixels, 14.3 cm) that covered most of the screen. See Fig. 1 for the entire trial sequence.

Touching the mask that was positioned where the target had been resulted in a food pellet, accompanied by a highly familiar positive auditory signal (“Excellent!”). Incorrect responses were followed by a highly familiar negative auditory signal (“D’oh!”) and a time-out of 5,000 ms. Trials were separated by intertrial intervals of 5,000 ms.

Monkeys received 120-trial training sessions with an SOA of 400 ms until they localized the target correctly on 90 % of trials within one session. This was followed by sessions with the SOA reduced to 200 ms, until monkeys again met the criterion. Twelve probe sessions were then administered, each consisting of 140 trials. Seventy trials in these probe sessions used the trained SOAs of 400 ms and 200 ms (35 trials each). The remaining 70 trials consisted of 10 trials of each of six SOAs encountered only in these probe sessions (100, 83.3, 66.7, 50.0, 33.3, 16.7 ms) and 10 “nothing” trials in which no target was shown. The “nothing” condition simply consisted of the background square displayed for 16.7 ms before onset of the four masks. On these trials, a target location was selected as in normal trials, but no target was presented. Responding to the selected location at test was rewarded as on normal trials. Throughout these experiments, the assignment of targets to the four corners of the screen was random with the constraint that each corner contained the target twice in each block of 8 trials, ensuring counterbalancing. The “nothing” condition provides a check of whether this counterbalancing affected the distribution of choices when the target was masked. We expected accuracy to be lower at shorter SOAs, consistent with decreased perceptibility of the target, and performance to be at chance on the “nothing” trials, confirming that when no target was presented, monkeys were unable to guess the scheduled location for the target.

Results and discussion

Accuracy varied with SOA (Fig. 2, univariate RM ANOVA: $F_{5,20} = 90.77$, $P < 0.001$). To test whether shorter SOAs were associated with lower accuracy, we ran a planned comparison between the longest and shortest probe SOAs (100 and 16.7 ms). To test whether monkeys responded to 16.7 ms SOA trials as if no stimulus had been presented, we ran a planned comparison of performance on this SOA to performance on the “nothing” condition. We chose this SOA (16.7 ms) because it was expected that the mask would be most efficient at this interval due to the monotonic nature of the efficiency of the chosen mask. Accuracy was significantly higher at the longest probe SOA of 100 ms than at the shortest probe SOA of 16.7 ms ($t_4 = 12.43$, $P < 0.001$), but remained above chance even at this shortest SOA as shown by a paired t test comparing the 16.7 ms condition to the “nothing” condition ($t_4 = 3.24$, $P = 0.032$).

When no target was shown, performance did not differ from chance (mean = 0.27, SEM = 0.017; $t_4 = 1.58$, $P = 0.19$), showing that monkeys could not guess the scheduled location of targets. Together these results show that visual masking does impair localization; however, even at the shortest SOA used, monkeys could still localize the target. See Supplementary Table 1 for response probabilities for each individual monkey at each SOA.

Experiment 2: Detection of masked stimuli

The masks used in Experiment 1 were chosen because they had previously been found to make targets phenomenally undetectable to human subjects at the 16.7 ms SOA (van Gaal et al. 2008). At this same SOA, monkeys in Experiment 1 were still able to localize targets. Thus, monkeys can localize stimuli that we expect human subjects would be unlikely to perceive. However, we cannot directly compare our data with the human data given potentially important procedural differences between our test and those used with humans. We therefore directly tested whether the monkeys perceived the masked stimuli at the shortest SOA in Experiment 2. In Experiment 2, we determined whether monkeys could report the presence or absence of identical targets across the same range of SOAs used in Experiment 1. If detection and localization dissociate in monkeys as they do in humans, then monkeys should be at chance of reporting the occurrence of targets at the shortest SOA, even though localization persisted at levels reliably above chance.

Methods

The subjects and apparatus from Experiment 1 were used again in Experiment 2. We also used the same target stimuli and masks, but two new response buttons were introduced. The masks no longer functioned as response buttons, and instead, monkeys used the two new response buttons to report whether or not a target had appeared. The full-trial sequence is shown in Fig. 3. In each session, half of the trials were “there” trials, and the other half were “not-there” trials. In “there” trials, a target stimulus was presented in one of the four corners followed by all four masks, just as in Experiment 1. In “not-there” trials, no target was presented. Instead, during the interval in which a target would have been presented in “there” trials, the screen displayed the gray background square. After this interval, the masks appeared as on other trials. The two new response buttons, red and green circles containing a white + or X, appeared concurrently with the four masks on all trials. Monkeys were required to touch the red button if the target had been absent and the green button if the target had been present, regardless of the location of the target. Correct and incorrect responses were reinforced in the same manner as in Experiment 1.

The two response buttons for the detection task did not always appear in the same locations. They were pseudorandomly distributed in a balanced manner among four possible positions with each configuration being used equally often and randomized independently of a target location, for a total of 12 possible response button configurations (Fig. 3). We randomized the location of the response buttons to prevent the monkeys from acquiring a habitual motor response to the occurrence of a target. This was important because we wanted to test visual detection in the absence of the type of habitual motor response hypothesized to underlie responding in Experiment 1.

Monkeys received training sessions of 120 trials and had to reach a performance level of 90 % correct on SOAs of 400 ms and 200 ms, as in Experiment 1, to advance to probe sessions. Monkeys then received 12 probe sessions of 120 trials, including 30 trials with an SOA of 400 ms and 30 trials with an SOA of 200 ms. The remaining 60 trials were evenly distributed among the six remaining SOAs. For each SOA, 50 % of the trials were “there”-trials, and the remaining 50 % were “not-there”-trials. Finally, to confirm that failure to

detect a target at a given SOA was actually a result of the rapid onset of the mask and not the brevity of the target, we ran an additional 12 sessions, which were identical except that a 200 ms gap was interposed between the offset of the target and the onset of the mask. Again, we ran planned comparisons of performance at the shortest and the longest SOA, and of performance at the shortest SOA to chance.

Results and discussion

Because this was a two-alternative detection task and therefore more susceptible to individual differences in bias and criterion level than are four-alternative choice tasks, performance was measured by signal detection analysis (Macmillan and Creelman 2005). Use of signal detection analysis on “there/not-there” tasks separates the influences of the subject’s response criterion from the subject’s detection capabilities, providing an unbiased estimate of the subject’s detection capabilities, expressed by d' (Hannula et al. 2005). A d' score of 0.0 reflects no discrimination between “there” and “not-there” trials, while larger values reflect more accurate discrimination. The accuracy of the monkeys was lower at shorter SOAs than at longer SOAs (Fig. 4; univariate RM ANOVA: $F_{5,20} = 33.20$, $P < 0.001$). Detection was significantly higher at the longest SOA (100 ms) than at the shortest SOA (16.7 ms: $t_4 = 9.97$, $P < 0.001$). In contrast to the successful localization performance seen in Experiment 1, monkeys were not able to detect target stimuli at the shortest SOA (Fig. 4; $t_4 = -1.00$, $P = 0.37$). However, monkeys were able to detect the same target when a 200 ms delay was interposed between mask and target even at the 16.7 ms duration (mean $d' = 1.19$; SEM = 0.10; $t_4 = 11.87$, $P < 0.001$). Thus, masking, and not brevity, was the critical determinant of whether targets were detected. See Supplementary Table 2 for response probabilities for individual monkeys at each SOA.

Two kinds of errors can be made in this detection test: false alarms and misses. False alarms are when monkeys report “there” in a “not-there” trial. Misses are when they report “not-there” in a “there” trial. If the masking procedure simply increased the general difficulty of the detection task, then we should observe equal numbers of false alarms and misses when accuracy is at chance, because the monkeys would be guessing. This was not the case. An analysis of errors showed an interaction between error type (false alarms and misses) and SOA (univariate RM ANOVA: $F_{5,44} = 11.86$, $P < 0.001$). SOA affected misses (univariate RM ANOVA: $F_{5,20} = 33.59$, $P < 0.001$), such that the proportion of misses at the longest SOA (100 ms) was significantly smaller than at the shortest SOA (16.7 ms: $t_4 = 7.72$, $P = 0.0015$). In contrast, the proportion of false alarms did not vary significantly with SOA (Fig. 5; univariate RM ANOVA: $F_{5,20} = 1.34$, $P = 0.29$). Therefore, the lower detection accuracy at shorter SOAs was due solely to higher frequencies of reporting the target as “not-there” when, in fact, a target had appeared. This shows that the monkeys were not responding randomly due to increased difficulty. Instead, the monkeys did not perceive the target and reported that. To further evaluate this interpretation, we tested whether reaction times differed as a function of SOA or task (detection and localization). Neither the main effect of SOA nor the interaction of SOA and task was significant (SOA: $F_{5,44} = 1.24$, $P = 0.31$; SOA $\times$ task: $F_{5,44} = 0.74$, $P = 0.60$), which is consistent with the hypothesis that monkeys solved the task in the same manner across all SOAs. Reaction times did differ between the two tasks, (task: $F_{1,44} = 255.48$, $P < 0.001$), as should be expected because in the detection task,

monkeys had to respond at a location different from where the target occurred, and the position of the correct responses button changed between trials.

General discussion

There were three main findings of this study. First, detection was poorer at shorter SOAs and was at chance at the shortest SOA tested (16.7 ms), demonstrating the effectiveness of the masking procedure. Second, the decrease in detection accuracy was driven by a selective increase in misses, demonstrating that the short SOA trials were systematically perceived by the monkeys as lacking a target. Third, localization accuracy was never at chance at any SOA, although it was lower at shorter SOAs. Together these results show that with an SOA of 16.7 ms, monkeys localized targets that they could not detect. These results appear to dissociate perception of targets from visually guided motor responses initiated by the targets, drawing a strong parallel in visual processing between monkeys and humans. One critique of this conclusion is that we used two different dependent measures with the two tests, proportion correct, and d' . While the appropriateness of this approach is well justified theoretically, we responded practically to this concern and converted the proportion correct scores from the localization task to d' scores, using the conversion tables of Macmillan & Creelman (2005). This resulted in a mean d' of 0.58 for localization at SOA = 16.7 ms. Expressed this way, localization was still significantly more accurate than detection at 16.7 ms ($t_4 = 6.17$, $P = 0.0035$).

Our results with intact monkeys support related conclusions from studies of blindsight in monkeys with V1 lesions (Cowey and Stoerig 1995). Whereas their study provided evidence that visually guided actions and visual detection could be dissociated through a neurological manipulation, the present study provided evidence that such a dissociation could also be achieved through a behavioral manipulation in intact monkeys. Thus, normal visual processing in monkeys engages at least two separate visual processing channels that carry different types of information. Under circumstances in which information normally carried by one processing stream is blocked, either through masking or brain damage, behavior can still be controlled by information carried by the remaining processing stream. It is possible that detection and localization are subserved by completely dissociable neural mechanisms and that this could be revealed by manipulating different variables or the nervous system directly. This is an intriguing question for further research. However, in the current experiments, the two processing streams were not fully dissociated; elimination of detection was accompanied by a reduction in localization accuracy, even though localization remained above chance. It is difficult to imagine circumstances in which manipulating SOA would not affect performance in both tasks. It may be the case that these two streams are only partially dissociable (Pisella et al. 2006). Nonetheless, it is clear that the visual representations that result from stimulation at the shortest SOA used here do not include information about the presence of a target, but do contain information about the location of the target.

A possible difficulty with interpretation of the present results is that localization accuracy was reliably higher than detection performance at all SOAs. Shorter SOAs might have impaired both detection and localization equally, causing detection to reach chance before localization simply because it started from a lower baseline level. According to this account,

there is no need to posit separate dissociable processing streams. This amounts to arguing that even with performance at chance, monkeys still had some residual ability to detect the targets and that the detection task was not sensitive enough to measure it. There are at least four reasons to conclude that this is unlikely to be the case and that the detection task was a valid measure of perception. First, we used an objective forced-choice task similar to the forced-choice tasks used with human subjects to measure low-level detection ability not normally measurable with subjective verbal reports (Hannula et al. 2005). Second, the monkeys were able to detect the targets at the shortest SOA when we inserted a 200 ms gap between the target and the mask, showing that the monkeys were adequately trained to report the presence of targets at 16.7 ms SOA. That they did not report targets suggests that they did not perceive them. Third, the fact that lower accuracy at shorter SOAs was caused by a selective increase in misses suggests that masking did not merely increase task difficulty or ambiguity. Increasing general difficulty or ambiguity would result in equal numbers of misses and false alarms, but short SOAs instead had the intended effect of decreasing perceptibility and selectively increasing misses. Finally, if decreasing SOAs merely increased general difficulty, we would have expected longer response latencies at shorter SOAs. By contrast, if monkeys confidently report “not-there” on short SOA trials, we would expect reaction latencies to remain constant, and indeed, we found no significant change in reaction times at different SOAs.

However, we acknowledge that the detection task may differ from the localization task in other ways that might affect accuracy. In the detection task, monkeys had to map their responses to stimuli displaced from the location of the target, and the location of the correct response varied from trial to trial. Searching for the correct response therefore required briefly maintaining the intended response in memory in the face of other visual input that could potentially overwrite memory of the sample. An independent information streams model also predicts differences in difficulty, so we cannot currently discriminate between these two explanations. These tasks were designed to contrast visual detection with the more automated response of visual localization. Therefore, we varied the location of the response buttons to avoid establishing an automated motor response in the detection task. So, although accuracy on the detection task was lower than on the localization task, and no detection task can ever fully rule out the possibility of preserved detection that is too faint to be measured, we conclude that the current task was a valid measure of the monkeys' detection abilities. We may make progress in future studies if we can equate visual search time without automating the detection task. It would be of interest to conduct an experiment in which the responses in the detection task were simplified by holding the positions of the response buttons constantly, but it would be important to determine whether this results in a habitual motor response akin to that in the localization task. Another potential future experiment could run the detection and localization task in an interleaved manner to cancel any effects of order of training.

The obtained results provide evidence for a dissociation of visual localization and visual detection in normal intact monkeys. Monkeys appear to localize stimuli that they do not perceive. These results cannot establish the existence of phenomenal vision in monkeys, but they do closely parallel the dissociation of conscious and unconscious vision found in humans.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.

The presentation sequence in the localization experiment. Trials were initiated by touching the *green square*, followed by a delay of 500 ms. Then, a target stimulus appeared in one of the four corners, followed by the four annuli that served as both masks and response buttons. The targets and masks were positioned such that they would share their outer and inner contours. Trials were separated by intertrial intervals (ITIs) of 5,000 ms (color figure online)

Fig. 2. Localization accuracy decreased as a function of shortened SOAs. *Error bars* are one standard error of the mean. For all SOAs, performance was above chance (*dashed line*)

Fig. 3.

The presentation sequence for the detection task. In this example, a target is shown, although this was the case on only half of trials. A *green* response button and a *red* response button were used to report presence or absence of the target, respectively. The *green* and *red* response buttons were always placed between two adjacent masks (i.e., *left-middle*, *right-middle*, *top-center*, *bottom-center*) and were placed pseudorandomly such that each appeared equally often in each of the four possible locations (color figure online)

Fig. 4. Detection accuracy, expressed as d' , as a function of SOA. Accuracy was lower at shorter SOAs, and at chance at the 16.7 ms SOA ($d' = -0.06$). Error bars are one standard error of the mean

Fig. 5.

Proportions of false alarms (trials on which monkeys reported “there” when no target had appeared) and misses (trials on which monkeys reported “not-there” when a target had appeared) at the tested SOAs. *Error bars* represent one standard error of the mean. The proportion of misses increased as a function of shorter SOAs, whereas the proportion of false alarms was not related to SOA