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RESEARCH ARTICLE

On doing two things at once: dolphin brain and nose coordinate sonar clicks, buzzes and emotional squeals with social sounds during fish capture

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ABSTRACT

Dolphins fishing alone in open waters may whistle without interrupting their sonar clicks as they find and eat or reject fish. Our study is the first to match sound and video from the dolphin with sound and video from near the fish. During search and capture of fish, free-swimming dolphins carried cameras to record video and sound. A hydrophone in the far field near the fish also recorded sound. From these two perspectives, we studied the time course of dolphin sound production during fish capture. Our observations identify the instant of fish capture. There are three consistent acoustic phases: sonar clicks locate the fish; about 0.4 s before capture, the dolphin clicks become more rapid to form a second phase, the terminal buzz; at or just before capture, the buzz turns to an emotional squeal (the victory squeal), which may last 0.2 to 20 s after capture. The squeals are pulse bursts that vary in duration, peak frequency and amplitude. The victory squeal may be a reflection of emotion triggered by brain dopamine release. It may also affect prey to ease capture and/or it may be a way to communicate the presence of food to other dolphins. Dolphins also use whistles as communication or social sounds. Whistling during sonar clicking suggests that dolphins may be adept at doing two things at once. We know that dolphin brain hemispheres may sleep independently. Our results suggest that the two dolphin brain hemispheres may also act independently in communication.

INTRODUCTION

Dolphins (*Tursiops truncatus*) find food using sonar. As they hunt for fish, the complex, asymmetrical, muscular nose makes brief, high-peak frequency click trains that are focused through the fatty melon-shaped forehead (Au, 1993; Jensen et al., 2009; Ridgway et al., 2014; Wisniewska et al., 2014). The clicks bounce off fish, returning echoes to the dolphin's ear (Au, 1993) where the cochlea converts the echoes into nerve impulses (McCormick et al., 1970, 1980). The brain analyzes these nerve impulses in several steps from the auditory nerve through the cochlear nucleus, lateral lemniscus, inferior colliculus, medial geniculate body and cerebral cortex. At the brainstem level, impulses cross to the opposite side of the brain through the olivocochlear bundle so that sound received by the left ear results in a greater response on the right side of the brain (Bullock et al., 1968; Bullock and Ridgway, 1972; Bullock and Gurevich, 1979; Supin et al., 1978). While the dolphin brain

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processes the echoes from the fish, dolphins hone in on the fish and make decisions about capture – fish or fowl, food or flotsam. In addition to sonar clicks, longer, lower frequency, whistle-like sounds occur in dolphin feeding groups (King and Janik, 2015).

Dolphins make sound with their nose. A single blowhole appears at the surface of the head. Underneath the closed blowhole or nasal plug lie paired nasal cavities. The underside of the nasal plug is also paired, closing off the two nasal openings. On the posterior margin of the underside of the nasal plug reside the left and right anterior phonic lips, critical for sound production (Cranford et al., 2011). Paired nasal plug muscles support the nasal plug and phonic lips (Mead, 1975). The nasal plugs and muscles are asymmetrical, the right side being always larger (Cranford et al., 2011). They control the pressurized airflow from the nasal cavities past the phonic lips. This pressurized airflow is essential for pulsed and whistle-like sounds (Ridgway et al., 1980).

While the nasal plug appears as a single unit at the surface of the dolphin head, the paired units below are important for sound production. The majority of sounds produced are lateralized. For example, we noticed movements and at times bubbling on the left side of the nasal plug before whistling and on the right side of the nasal plug before pulsing. Therefore, when we wish to train a dolphin to respond with a whistle, we tap the left side of the blowhole. For pulsed sound, we tap the right side (Ridgway et al., 2009). We have never tried to train the dolphin to reverse sides with their sounds; however, Cranford et al. (2011) showed that minorities of observed pulsed sounds were on the left. Most observations indicated that whistles are generally produced from the left side, and pulses from the right side. In studies with suction cup hydrophones attached to left and right sides of the head, Madsen et al. (2013) found that all pulses were produced on the right and all whistle-like sounds on the left. We do not know of any reversal of this situation. Pressure rises in both nasal cavities simultaneously (Ridgway et al., 1980; Cranford et al., 2011), thus the plugs must be capable of releasing airflow independently past right and left phonic lips.

We wanted to study the coordination and timing of the different dolphin sounds as they captured fish. To do this, we trained dolphins to wear cameras temporarily attached to their foreheads. The cameras focused on the dolphin rostrum recording sound and video so that the instant of capture could be seen and heard. We also wanted to record sound and video with a broadband hydrophone and camera near the fish. From these two perspectives, we aimed to study the time course of dolphin sound during fish capture and to identify the instant of fish capture in relation to the sounds produced. The first two phases of fish capture, sonar clicking and the terminal buzz (TB), have received a good deal of attention in *T. truncatus* and other cetaceans (Au et al., 2013; Wisniewska et al., 2014). The victory squeal (VS) is a third phase (Ridgway et al., 2014). This

List of abbreviations

BIS	bispectral index
DTI	diffusion tensor imaging
MRI	magnetic resonance image
TB	terminal buzz
VS	victory squeal

third phase has not received as much attention with respect to fish capture. Usually the VS has been included with the TB. For example, DeRuiter et al. (2009) described the TB of porpoises, *Phocoena phocoena*, beginning about 500 ms before fish capture and going on for 800 ms after. We sought to refine our understanding of the VS and its relation to the TB and to fish capture. Could the timing of the VS be consistent with an emotional response following dopamine release, as suggested previously (Ridgway et al., 2014)?

Lilly and Miller (1961) showed that a solitary dolphin in the laboratory could simultaneously emit pulsed sounds and whistles. Previously, no context has been provided for simultaneous whistling and clicking. As a further goal of this study, we wanted to know if simultaneous whistling and clicking occurred while dolphins were engaged in an important sonar task – finding food.

MATERIALS AND METHODS
Study subjects
We adapted seven dolphins aged 3–50 years to wearing cameras (GoPro Hero3, Hero3+, Hero4 silver). None of these animals was employed in studies reported previously (Ridgway et al., 2014). Five of the seven dolphins were born at Navy Marine Mammal Program facility and never caught fish in the wild. The oldest animal was taken from the Mississippi management area of the Gulf of Mexico in 1971 at an estimated age of 6 years (Table 1).

We conducted 680 fish capture trials (Table 2) with seven dolphins (Table 1) wearing cameras (Fig. 1). The cameras were attached temporarily by rubber suction cups. The cups were readily accepted by the dolphins, stayed on while the animal swam rapidly, and caused no injury or apparent discomfort to dolphin skin. Suction cups have previously been used for attachment of acoustic recorders and tracking devices to cetaceans (Johnson et al., 2006; Wisniewska et al., 2014). From the dolphin's forehead, the camera recorded the search, approach and capture of fish. The camera recorded sound with a bandwidth of 16 kHz. For a broader frequency range, a hydrophone (B&K 8101, Brüel & Kjær, Denmark, with Dodotronic UltraMic250 amplifier/digitizer) recorded sound from behind the fish within the dolphin's narrow sonar beam (Au, 1993; Finneran et al., 2014). The far-field digitized sound from the hydrophone was analyzed with SeaPro software (CIBRA, Italy). The camera sound was imported into Audacity and displayed with Adobe Audition.

The initial data were collected in an 18×9 m net enclosure in San Diego Bay. Trials began with the dolphin, head out of the water, attending to its trainer at one end of the enclosure. At the opposite end, the recording hydrophone was lowered to a depth of between 1 and 2 m. The fish was
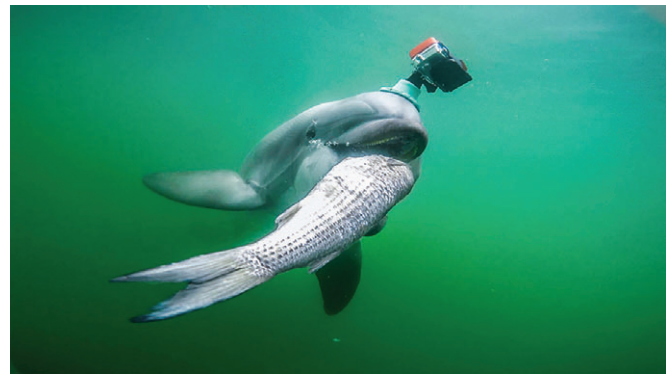
Fig. 1. View from the camera near the far-field hydrophone as the dolphin captures a mullet. The camera attached temporarily to the dolphin's forehead by a rubber suction cup is positioned to record the instant of fish capture. During more than 90% of trials, dolphins searched with sonar clicks as they swam towards the fish location (Table 2). Inter-pulse intervals in the first phase, the sonar click phase, were long and varied, in agreement with the earlier findings of Morozov et al. (1972). About 0.4 s before capture, the dolphin's clicks become more rapid to form a second phase, the TB (Figs 2 and 3). At or just before capture, the buzz turns to an emotional squeal, the victory squeal (VS), which may last 0.2–20 s after the dolphin first makes contact with the fish.

placed 12–15 m from the dolphin, near the hydrophone to capture the dolphin's narrowly projected sonar beam as it approaches the fish. To begin each session, the trainer stationed the animal while the fish was inserted 1–2 m below the surface. The trainer released the dolphin to find the fish.

In our initial tests, other dolphins were only 20 or 30 m away. We wanted to have more certainty that whistles made during clicking were from our test subjects and not from other dolphins. The two older subjects (BLU, SPL) were experienced in swimming alongside boats out at sea. We moved their trials 750 m to 1 km away from any other dolphins in the open waters of San Diego Bay. Each animal fished alone, well away from other dolphins. Trials began with the dolphin, head out of the water, attending to its trainer at boat one. At the bow of boat two, 20–30 m away, the far-field hydrophone and camera were placed at 1–2 m depth. The fish was then placed in front of the hydrophone and camera at the same depth to collect clicks of the dolphin's narrowly projected sonar beam as it approached the fish for capture. To begin each session, the trainer stationed the animal while the fish was inserted 1–2 m below the surface. The trainer released the dolphin to find the fish. One series of tests was done with SPL alone in an above-ground 6×12 m pool as a second confirmation that simultaneous sonar clicks and whistles were from the same individual.

RESULTS
Similar to previous studies (Morozov, 1972; Jensen et al., 2009; Wisniewska et al., 2014), we found that the interval between dolphin sonar clicks decreased as the animal approached the fish. The three sounds associated with dolphin fish capture (sonar clicks, TB and the VS) were analyzed for each trial (Table 2).

Table 1. Characteristics of the seven bottlenose dolphins (*Tursiops truncatus*) used in the experiments

| ID	Sex	Length (cm)	Mass (kg)	Age (years)	Date of birth	Origin
KNG	M	227	132	3.5	07/01/12	MMP
MGU	M	227	143	3.8	29/09/11	MMP
LNC	M	226	138	4.1	01/06/11	MMP
SWD	M	223	161	6.3	29/03/09	MMP
LRK	F	257	198	11	30/07/04	MMP
SPL	F	251	188	33.1	15/06/82	MMA
BLU	F	251	201	50.1	15/06/65	MMA

Five of the animals were born at facilities of the United States Navy Marine Mammal Program (MMP), and two were collected from the wild in the Mississippi Management Area (MMA) in the Gulf of Mexico. ID, dolphin individual identification; M, male; F, female.

Table 2. Results from net enclosures, pool and open water trials

|	Open water/pool	Sea pen enclosure	Total
Total trials	226	454	680
Click trains (N)	218	420	638
Click trains (%)	96.5	92.5	94.5
Terminal buzzes (N)	221	420	641
Terminal buzzes (%)	97.8	92.5	95.2
Victory squeals (N)	202	404	606
Victory squeals (%)	89.4	89.0	89.2
Whistles/click trains (N)	21	n/c	21
Whistles/click trains (%)	9.3	n/a	9.3

N denotes number; for whistles/click trains, N denotes occurrence of simultaneous whistle and sonar clicks; n/c, not counted; n/a, not applicable. Although numerous overlapping whistles and clicks were observed in trials in enclosures, these were not totalled because of close proximity of other dolphins only 20 or 30 m away.

Our observations identify the instant of fish capture. Our video and acoustic evidence refines the time course of previous sound recordings from toothed whales in the wild and in captivity. Our observations support the idea that head jerks recorded from beaked whales and delphinids carrying acoustic tags correlate with eating prey (Johnson et al., 2006, Wisniewska et al., 2014). Fig. 2 demonstrates head jerk actions occurring simultaneously with the instant of fish capture. These squeals may be a reflection of emotion or may serve to communicate the presence of food to others in the group (Ridgway et al., 2014; Wisniewska et al., 2014). Squeals differ from sonar clicks and TB in that their peak frequencies sweep and vary considerably over time (Figs 2, 3, Movie 1). In a few trials, dolphins rejected the fish after a TB. On rejection, the animal gave only a brief VS or no VS.
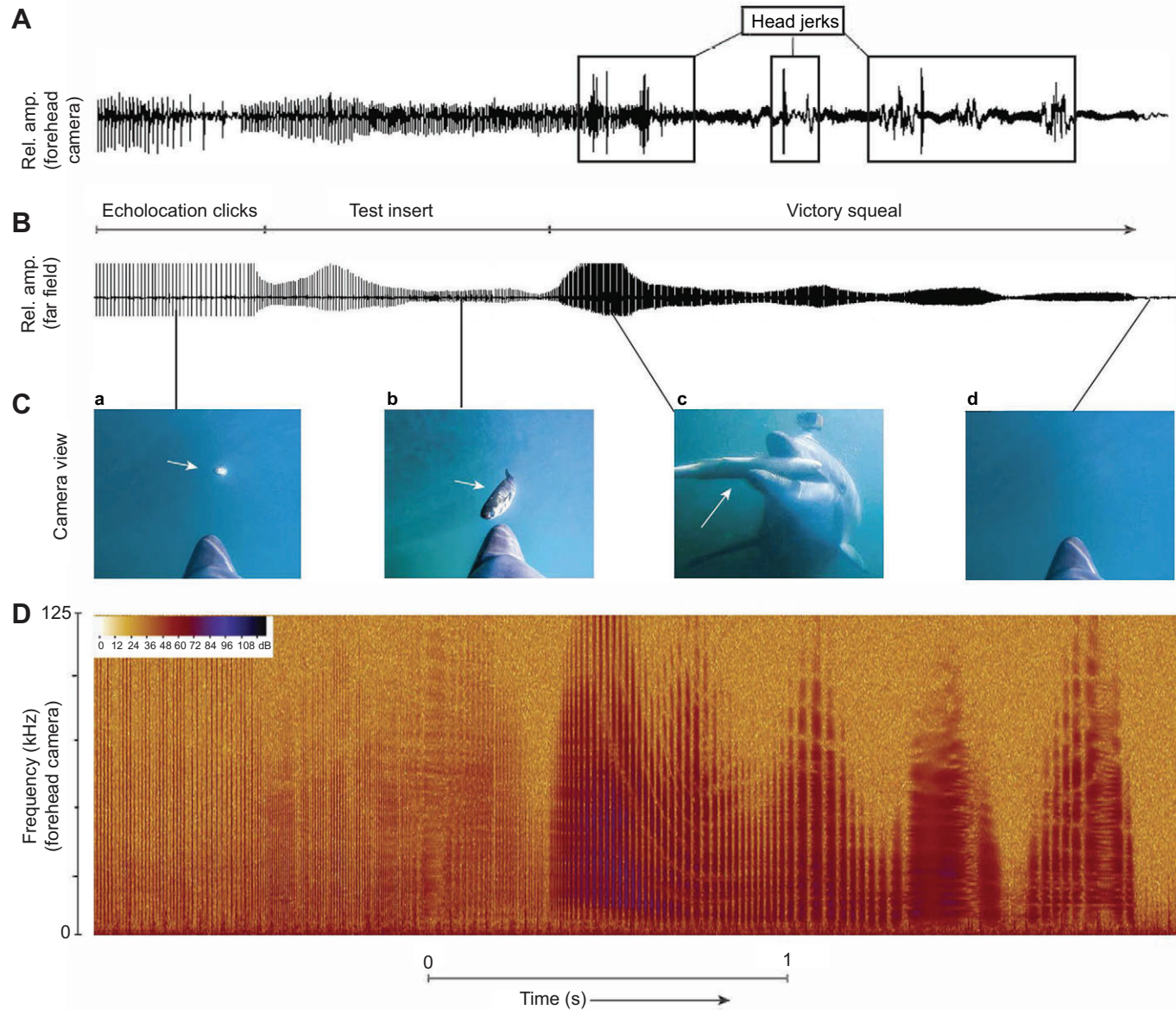
Fig. 2. Dolphins carried a camera on their foreheads for recording. (A,C) Video and sound were recorded during approach and capture of fish. Simultaneously, a camera and hydrophone in the far field behind the fish recorded video and broadband sound (B,Cc,D). (C) Left to right: (a) view from forehead camera of fish (white arrow) in the distance; clicks are recorded on forehead and far-field cameras and hydrophone; (b) closing in on fish, TB; (c) view from far-field camera with fish in dolphin's mouth, victory squeal from both cameras and hydrophone. As the dolphin eats the fish, head jerks are recorded on the forehead camera microphone (A), but not on the far-field hydrophone (B,D). (Cd) View from forehead camera showing dolphin rostrum as the animal moves away clicking. Relative amplitude (in dB) is shown in the inset in D. Rel. amp., relative amplitude.
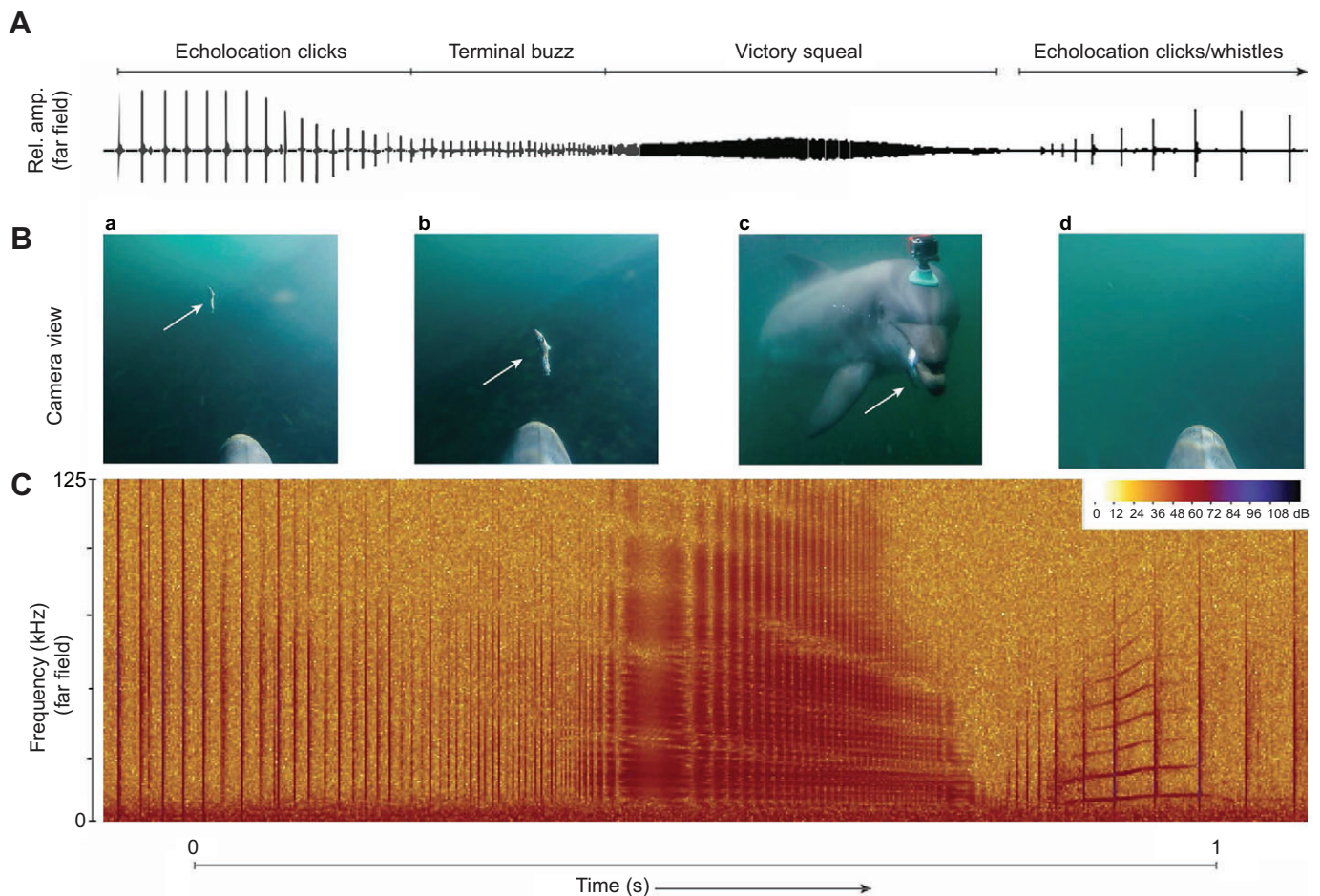
Fig. 3. Sounds of fish capture with simultaneous whistle and echolocation following the capture. (A) A hydrophone in the far field near the fish recorded broadband sound as the dolphin approached the fish. Dolphins carried a camera recording video during approach and capture of fish (Ba,b,d). Simultaneously, a camera (Bc) and hydrophone (A,C) in the far field behind the fish recorded video and broadband sound. The forehead camera recorded a rostral view (Ba,b,d) from the perspective of the dolphin during foraging. (B) From left to right, the dolphin uses clicks (a) to discriminate between its surroundings and prey, indicated by the white arrow. Once a fish is near, the sonar clicks transition into a terminal buzz (TB) that refines the information the dolphin receives back from the echoes bouncing off the fish (A,Bb,C). As the dolphin nears capture, the TB turns into an emotional response, the victory squeal (VS), just before fish capture (Bc) that lasts the duration of prey ingestion. Clicks and a simultaneous whistle follow as the dolphin moves away and remains vigilant(A,Bd,C). The longer interpulse intervals after fish capture suggest that the dolphin is concentrating more on distant targets. Relative amplitude (in dB) is shown on inset on upper right in C.

Although many overlapping whistles and clicks were recorded during the 454 trials conducted in sea pen enclosures, we did not quantify these results due to the close proximity of surrounding dolphins, only 20–30 m away. On some trials, we turned the camera on the forehead to face the blowhole (Fig. 4). These trials showed nasal plug movement simultaneous with overlapping whistles and sonar clicks.

During open water and pool trials, the dolphin was alone, 750–1000 m away from any other dolphin, or by itself in a pool (Fig. 5). During these fish capture trials, simultaneous production of sonar clicks and whistles were recorded for 9.3% of trials (Table 2).

DISCUSSION

A unique finding of our study concerns the order and timing of the three distinct sounds of the dolphin during hunting and capturing fish. Our study is the first to match sound and video from the dolphin with sound and video near the fish. This allowed us to identify the instant of fish capture. This also allowed us, for the first time, to identify three consistent acoustic phases of fish capture. Sonar clicks locate the fish. About 0.4 s before capture, the dolphin clicks become more rapid to form a second phase, the TB. At or just before

fish capture, the TB turns to emotional squeal – the VS – bursts of pulses that vary in duration, peak frequency and amplitude.

The VS occurs after or just as a dolphin contacts fish. A VS also occurs when dolphins receive a signal from their trainers that they have responded correctly. Dopamine, the neurotransmitter that helps control the brain's reward and pleasure centers is present in cetacean brains. The timing of the VS is consistent with a response after dopamine release (Ridgway et al., 2014). The TB begins around 400 ms before fish contact. At times, our dolphins rejected a fish during or just after the TB. These rejections probably account for the overall number of VS being lower than the TB (Table 2). We suggest that the decision to take the fish is made during the TB. This is consistent with previous ideas about the function of the TB (cf. Johnson et al., 2006; DeRuiter et al., 2009; Wisniewska, 2014). Also, this is consistent with neural time measurements (Ridgway, 2011; Ridgway et al., 2012). We suggest that this decision causes brain dopamine release, triggering the VS that most often lasts 500 ms to 2 s (Figs 2, 3, Movie 1).

Dolphins use sonar clicks to hunt for food. Whistles recorded from feeding groups are regarded as social communication between group members (Acevedo-Gutiérrez and Stienessen, 2004; King
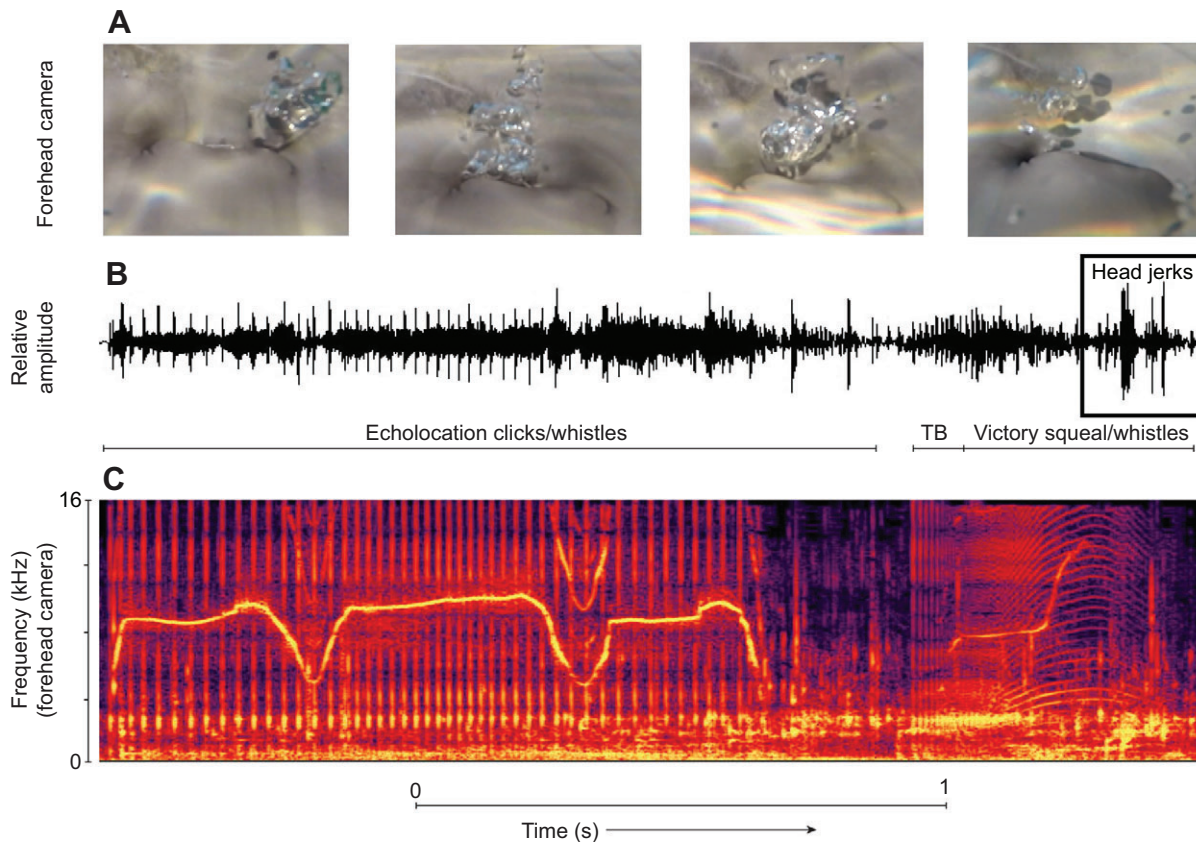
Fig. 4. Sounds of fish capture with simultaneous whistling, sonar pulses, and blowhole movements. (A) As the dolphin actively pursues prey, the plug appears to move in a fluid motion from left to right while the dolphin simultaneously produces whistles and sonar clicks prior to emitting a complex victory squeal on getting the fish (A,B,C) and eating it (head jerks). TB, terminal buzz. Younger animals are more likely to produce bubbles and higher frequency whistles compared with older dolphins. In the majority of trials, regardless of age, bubbles and/or whistles were not recorded.

and Janik, 2015). Before our study, it was not known that one individual could whistle and simultaneously use sonar clicks in finding fish. The dolphin must focus on its most import life task, finding food. Yet, during this important focus, while using sonar clicks to hunt, dolphins can simultaneously make sounds reckoned to be for social communication. We think our finding has implications for understanding how the cetacean brain and muscles control sound production.

Dolphins make all of these sounds with their nose (Ridgway et al., 1980; Amundin and Anderson, 1983; Cranford et al., 2011; Madsen et al., 2013) using a pair of right and left lips. The left and right phonic lips and some of the voluntary muscles that control them are different in size. The right side is always larger (Mead, 1975). The preponderance of observations show that dolphins make pulsed sounds on the right side of the nose and whistles on the left (Ridgway et al., 2009; Madsen et al., 2013). Cranford et al. (2011) observed a minority of pulsed sounds on the left. We know of no incidence of whistles from the right. Our observation of whistling during echolocation raises some questions about brain organization and control of sound production. Auditory, visual and somatosensory stimuli presented to one side of the animal all give larger responses on the opposite side of the brain (Bullock et al., 1968; Bullock and Ridgway, 1972; Ladygina and Supin, 1977; Supin et al., 1978; Ridgway and Carder, 1993). Crossed connections are characteristic of the mammalian brain. The brain's right hemisphere controls the voluntary muscles on the left side of the body, while the left hemisphere controls

the muscles on the right side (Kandel et al., 2000). We do not know of any anatomical or physiological evidence that the dolphin brain departs from this mammalian trait. In light of our present understanding, we must assume that our fishing dolphin is using both brain hemispheres in order to click and whistle simultaneously.

The dolphin's sounds may be key to understanding brain organization and how dolphins function during their unihemispheric or 'half brain' sleep. Dolphins have large brains with two hemispheres that are able to sleep at different times. Studies using the electroencephalogram (EEG) have shown that large, slow brain waves of sleep may appear on one brain hemisphere, while low-level, fast activity characteristic of waking may appear on the other brain hemisphere. In sleeping humans and other terrestrial mammals, sleep EEG and awake EEG is seen simultaneously on both hemispheres of the brain. Dolphin unihemispheric sleep is one of the most frequently replicated dolphin physiological phenomena (McCormick, 1969; Ladygina and Supin, 1977; Mukhametov et al., 1977; Supin et al., 1978; Mukhametov et al., 1987; Ridgway, 2002; Howard et al., 2006; McCormick, 2007; Lyamin et al., 2007, 2008). Unihemispheric sleep was demonstrated not only with EEG but also with the bispectral index (BIS) monitor (Howard et al., 2006). BIS, EEG or behavioral monitoring of eye state have all shown that one hemisphere may be awake while the other sleeps (reviewed in Lyamin et al., 2008). Dolphins, at least briefly, can sleep with both hemispheres (Ridgway, 2002; McCormick, 2007); however, the
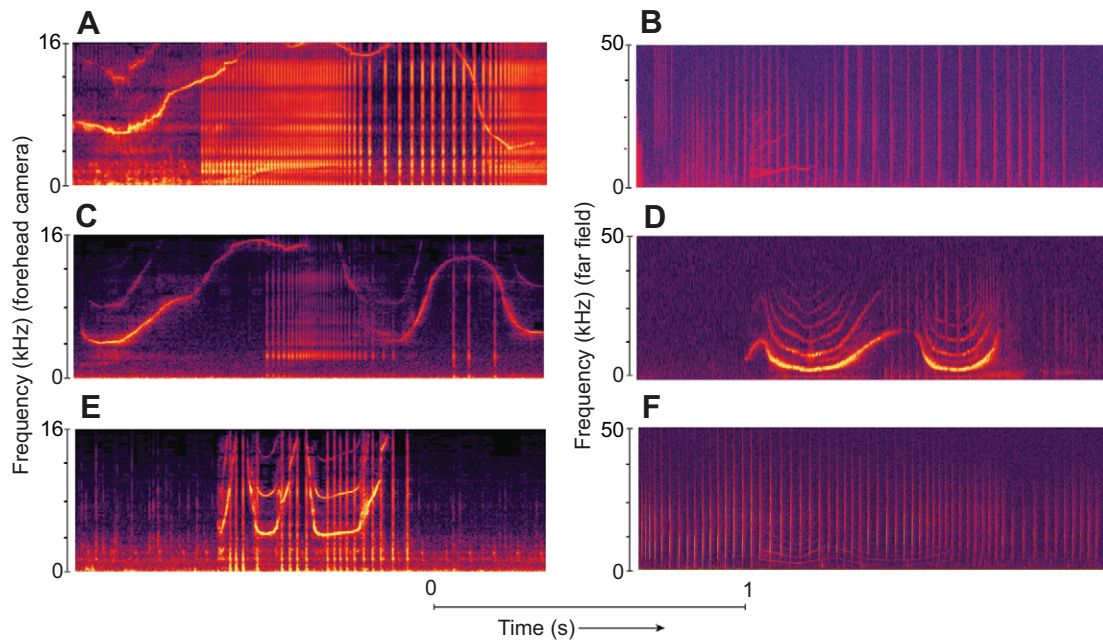
Fig. 5. Dolphins BLU and SPL participated in open water trials in San Diego Bay. The trials took place approximately 750 m away from other dolphins; SPL, unaccompanied, participated in 3 days of pool trials. Overlapping whistles and sonar clicks were observed in various trials. Six of these examples are displayed; three recordings are from the hydrophone in the far field (B,D,F) and the remaining three (A,C,E) are from the forehead camera. These recordings show periods of simultaneous sonar click production and whistling. The structural forms of the whistles vary, but this simultaneous sound production shows that one dolphin is capable of producing two distinct sounds at once.

vast majority of sleep is apparently unihemispheric (Mukhametov et al., 1977; Supin et al., 1978; Lyamin et al., 2008). The corpus callosum is the main communication link between the two cerebral hemispheres. In cetaceans, this link is very small (Tarpley and Ridgway, 1994; Keogh and Ridgway, 2008). Limiting excitatory input from the awake hemisphere, this small corpus callosum may help dolphins to transition sleep from one brain hemisphere to the other, as is seen with EEG or BIS recording. Also, there is a complete crossing of the optic nerve at the chiasma so that the left eye projects to the right side of the brain and vice versa (McCormick, 1969; Tarpley et al., 1994). This complete crossing of the visual system might also facilitate unihemispheric sleep. Usually the left eye is closed when the right brain is asleep and vice versa (McCormick, 2007; Lyamin et al., 2008). Sound production during sleep has been studied very little.

For example, frequent whistle exchanges between mothers and calves are well known (Tyack, 1997). During their first month or two of life, dolphin calves swim continuously with their mothers. Mother and calf apparently get their sleep underway (Lyamin et al., 2005; Sekiguchi et al., 2006; Lyamin et al., 2007; Hill et al., 2008; Cirelli and Tononi, 2008). Yet there are no reports of around-the-clock observations of mother and calf whistle exchanges.

Sleep is essential for all animals. Even flies sleep. There is no clear evidence of a species that does not sleep (Cirelli and Tononi, 2008). In cetacean species studied with EEG, unihemispheric sleep has been documented in dolphins (*T. truncatus*) and porpoises (*P. phocoena*) swimming continuously (reviewed by Lyamin et al., 2008; Cirelli and Tononi, 2008). Some cetaceans never stop swimming and we must presume that they also get sufficient sleep without stopping. McCormick (1969) observed constant swimming in the Dall porpoise (*Phocoenoides dalli*). River dolphins, *Platanista gangetica*, swam continuously (Pilleri, 1979). They clicked almost continuously except for brief interruptions of 4–60 s.

Pilleri (1979) interpreted these brief interruptions as brief sleep periods that added up to about 7 h in a 24 h day. Sekiguchi et al. (2006) also noted click-type sounds from continuously swimming dolphins during apparent sleep. Sonar clicks of swimming dolphins are often missed because they are focused in a narrow beam ahead of the dolphin (Au, 1993; Finneran et al., 2014). When our study dolphins turned their heads to the side or downwards, sonar clicks were not recorded on the far-field hydrophone near the fish. To assure collection of all clicks, Branstetter et al. (2012) used eight hydrophones around the circumference of a netted bay dolphin enclosure. During this study with eight hydrophones, dolphins continuously clicked and responded to echoes around the clock. The dolphins accurately reported the presence of target echoes presented frequently and randomly. On receiving an echo from one of its sonar clicks, the dolphin altered its normal circular swim, then swam to and pressed a paddle at the edge of its enclosure to confirm the detection. One dolphin did this task for 15 continuous days without interruption (Branstetter et al., 2012).

From the above, we conclude that dolphins can click while sleeping. We do not know if a dolphin wakes after an echo return that requires it to make a decision and a response as Branstetter et al. (2012) observed. We have not heard whistles or pulse bursts from sleeping dolphins – only sonar clicks. Our results showing simultaneous clicking and whistling link current research on sound production and brain anatomy with older studies showing separate dolphin brain loci for the two sound types (Bullock and Ridgway, 1972; Ladygina and Supin, 1977; Supin et al., 1978). Bullock and Ridgway (1972) found areas of temporal cortex (Fig. 6) that responded only to low frequency, slowly rising sounds like dolphin whistles. In humans and other terrestrial mammals auditory areas are in the temporal cortex. Recently, diffusion tensor imaging (DTI) has shown auditory connections to dolphin temporal cortex (Berns et al., 2015). Ladygina and Supin (1977) and Supin et al. (1978) used clicks to map auditory responses of the dolphin cerebral
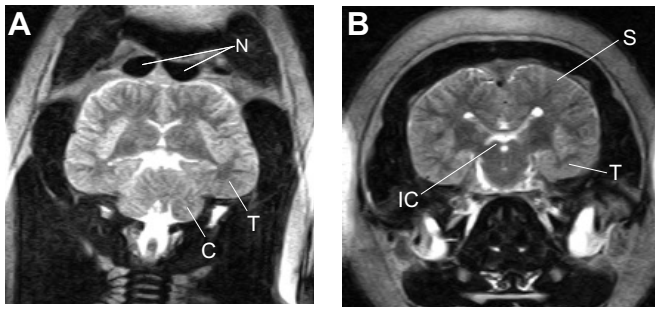
Fig. 6. Two magnetic resonance images (MRI) of the head of a live dolphin from the study of Ridgway et al. (2006). (A) Horizontal MRI section parallel to the long axis of the body. Here we can see ventricles (appearing as white areas in the brain scans), cerebellum and large dark fiber tracts running towards temporal cortex and forward towards the frontal cortex. The right and left nasal cavities appear just across the thin bone ahead of the frontal cortex. (B) Frontal MRI section, perpendicular to the long axis of the body. T, temporal cortex; S, superior auditory cortex; N, nasal cavities; C, cerebellum; IC, inferior colliculus. The scan was done 10 years ago, and the dolphin still lives under our care. Because adult *T. truncatus* are too large for high power (3 T) closed MRI scanners, a low-power 0.5 T open scanner had to be used. Even in this low-resolution scan, many features of the brain are evident.

cortex. Their studies found a large area of auditory cortex in an unusual (compared with other modern mammals) dorsal location (Fig. 6). Some of the click stimuli resulted in unusually rapid responses in this dorsal auditory cortex – as fast as 6 ms. It is possible that the dorsal auditory area exposed by Ladygina and Supin (1977) and Supin et al. (1978) is specialized for sonar analysis, and temporal auditory areas are specialized for longer, slower whistle-like sounds for social communication (Bullock and Ridgway, 1972). In awake animals, the great majority of clicks and pulsed sounds are produced on the right side of the nose and all the whistles come from the left (Madsen et al., 2013). Cranford et al. (2011) found that some clicks of awake dolphins (*T. truncatus*) were produced on the left. Therefore, either hemisphere might control clicking. This might explain the observation of continuous clicking for many days (Branstetter et al., 2012) while the animals alternates sleep in one hemisphere and then the other.

We doubt that dolphins have the ability to simultaneously whistle and produce sonar clicks during their half-brain sleep. If they do this, it may be due to the dolphin's ability to transfer control over sound production from one hemisphere to the other. Such a transfer would require anatomical connections that have not been observed. Alternatively, both hemispheres may be capable of whistling and clicking through active subthalamic mechanisms. Researchers have previously found that unihemispheric sleep includes the corticothalamic areas of the brain (Ladygina and Supin, 1977; Supin et al., 1978). Furthermore, the studies of Branstetter et al. (2012) and Ridgway et al. (2006, 2009) demonstrated that dolphins might be able to respond to echoes or to presented tones continuously, despite the necessity for sleep. They get essential sleep critical for homeostasis and for maintaining awareness by engaging in unihemispheric sleep. The inferior colliculus is located at a subthalamic level, which may further facilitate the production of clicks and reception of echoes during sleep. Also at a subthalamic level is an especially large elaboration of periaqueductal gray – the nucleus ellipticus. Lilly (1964) proposed the nucleus as a site of respiration control. This large nucleus of the midbrain, found only in elephants, elephant seals and cetaceans, may act as a specialized vocal pattern generator (Manger, 2006; Stoeger and Manger, 2014). However, it is likely that decisions about responding to sonar targets

must be made at the level of the cerebral cortex. Decisions to make or respond to whistles and other social sounds must also reside at the cortical level (Platt and Glimcher, 1999). It is likely that there are connections in the dolphin brain that are yet to be explained. These might be explored further with DTI. Such studies have already begun (Berns et al., 2015) and have shown auditory connections to temporal cortex (Fig. 6) identified by Bullock and Ridgway (1972) as whistle sensitive.

Many consider whistles as communication or social sounds (Au, 1993; Musser et al., 2014; King and Janik, 2015). Their simultaneous use while searching with sonar clicks suggests that dolphins may be adept at doing two things at once – making decisions about food capture and communicating with other animals in the process.

Our observations refine the time course of the three distinct sounds of fish capture. Our observations identify the instant of fish capture. Our video and acoustic evidence refines the perspective of previous sound recordings from toothed whales in the wild and in captivity. As they contact and eat prey, animals produce squeals – pulse bursts that vary in duration, peak frequency and amplitude (Figs 2, 3, Movie 1). These squeals may be a reflection of emotion (Ridgway et al., 2014), may affect the prey to ease capture and ingestion, and may serve to communicate the presence of food to others in the group (Johnson et al., 2006).

We clearly show the instant of fish capture within the dolphin's train of sound (Figs 2, 3, Movie 1). Our simultaneous video and acoustic evidence reinforces the view that head jerks recorded from beaked whales and delphinids carrying acoustic tags coincide with consuming prey (Johnson et al., 2006; Wisniewska et al., 2014). We recorded three different sounds during the pursuit and capture of fish. The dolphin uses sonar clicks to locate fish in the distance. A TB signals final closure and the VS ensues as the dolphin contacts and eats the fish. Additionally, we found the first instance of dual sound production in dolphins using sonar to find fish while whistling.

Cetaceans spend most of their lives unseen in the ocean depths. Seeing and hearing cetaceans in their natural environment can reveal much. With these methods, it is possible to attain acoustic data both in the near field, from the perspective of the dolphin, and in the far field from clicks projected at the fish. This is a new strategy for recording delphinid acoustics. The forehead camera records sound and visual data from the dolphin's perspective. This perspective offers an innovative new way to identify the instant of fish capture or other behavior. In the future, even smaller cameras and sound recorders will allow better understanding of cetaceans as they spend most of their lives unseen in the deep ocean.

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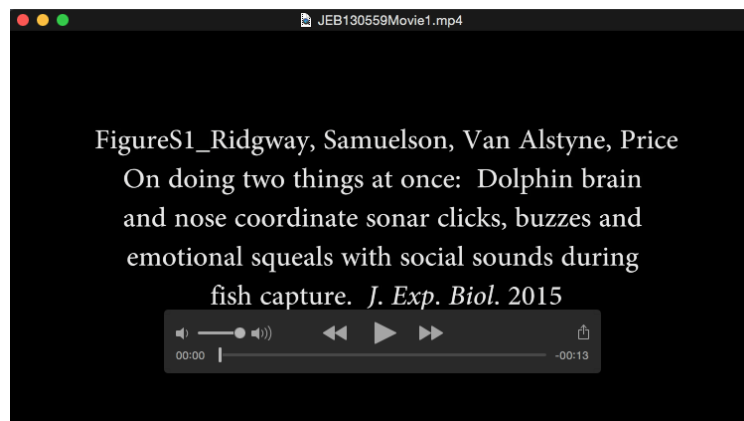
Movie 1. Video of fish capture with sound.